

REVISION OF THE GENUS MYRMOTERAS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT. The Asiatic formicine ant genus *Myrmoteras* is revised in full, with descriptions of ten new species and redescrptions of the eight previously described species here considered valid; *M. kemneri* is provisionally synonymized with *M. barbouri*. Among the new species are the first records of *Myrmoteras* from India and Sulawesi.

Two subgenera are recognized: in the subgenus *Myrmoteras* (with seven species in two species-groups) a pair of long trigger hairs extends from the labrum; in the new subgenus *Myagroteras* (with eleven species in four species-groups) the trigger hairs are absent. Cladistic analysis supports the informal species-group divisions and (if it is assumed that loss of palpal segments is more probable than regain) the monophyly of both subgenera.

INTRODUCTION

The tribe Myrmoteratini, containing the single genus *Myrmoteras*, is a small group of infrequently collected formicine ants with a distribution restricted to tropical Asia. With their oddly shaped heads, huge eyes, and extraordinarily long mandibles, *Myrmoteras* are unquestionably among the most bizarre ants in the world fauna.

Myrmoteras has been regarded as relatively primitive since Emery (1925). Characters considered ancestral for the Formicinae include the asepalous proventriculus (Eisner, 1957) and the wing venation (Brown and Nutting, 1949). Obviously derived characters are numerous, however, and include the most conspicuous and distinctive morphological features. Notable here is the elongation of the mandibles, which are linear with approx-

imate insertions. The back of the head has become widened, apparently to accommodate relatively massive mandibular muscles, and a distinctive occipital lobe has formed. In addition, there has been the development, in some species, of trigger hairs extending from the labrum forward between the mandibles.

These morphological characters relate in large part to a specialized mode of foraging behavior. *Myrmoteras* workers and queens are capable of opening their mandibles about 280°, wider than has been observed for any other ant (Figs. 1, 2). In *M. toro*, a species I have observed in Sulawesi, workers seize active, soft-bodied prey by snapping their mandibles forward from the fully open position. This is essentially the same prey capture technique as that used by ants in other subfamilies of the Formicidae: odontomachinae ants (Ponerinae) and dacetinae ants (Myrmicinae). All three groups depend heavily or entirely on the capture of large or agile prey by solitary foragers, without the benefit of recruitment.² In addition, R. W. Taylor (CSIRO, Canberra, Australia) has discovered several species of Leptanillinae which are also trap-jaw ants.

The constellation of anatomical and behavioral characters that bear on trap-jaw predation are apparently apomorphies in the respective subfamilies of each group

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² In certain trap-jaw species the trap-jaw apparatus has been modified secondarily to serve more effectively for defense (Carlin, 1983). This has not occurred in *Myrmoteras* species.

containing trap-jaw ants. That these traits have recurrently coevolved suggests that they represent an 'adaptive syndrome,' in other words, a suite of characters likely to evolve together or in some sequence to produce a more or less narrowly defined phenotype with specific functions (in this case the trap-jaw apparatus). The prevalence of odontomachine and dacetine ants in tropical ecosystems around the globe attests to the widespread significance of the niche open to ants that have convergently developed trap-jaw predation. Indeed, *Myrmoterias* ants are probably more ecologically important in tropical Asia than the infrequency with which they have been collected suggests: those localities at which collecting has been most intense in recent years, such as Gunung Mulu National Park, are now known to harbor several species.

RELATIONSHIPS

The species of *Myrmoterias* fall into two distinct groups, one of seven species (subgenus *Myrmoterias*) and one of eleven (subgenus *Myagroteras*) which can be readily distinguished by labral characters. Females in the subgenus *Myrmoterias* have a pair of prominent trigger hairs that originate from the middle of the dorsal face of the labrum. The species of *Myagroteras* lack long, prominent trigger hairs (although there are two much shorter and more widely separated labral hairs), and the dorsal surface of the labrum is more or less rounded, not coming to a distinct medial point. Although not noted by previous authors, these characters are easily recognized even in the field, and are apparent in illustrations of head structure in previous taxonomic treatments of *Myrmoterias*, for example in plate 6 of Creighton (1930). Another conspicuous character distinguishing *Myagroteras* from *Myrmoterias* is the presence of a longitudinal sulcus extending between the frontal area and medial ocellus in all *Myagroteras* species except *M. insulcatum*. In the subgenus *Myrmoterias* the sulcus is invariably

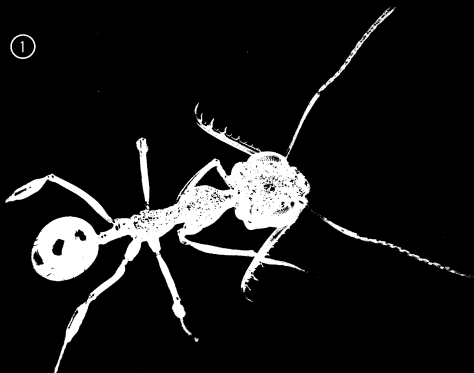
very feeble or absent. Gregg (1956) indicated that *Myrmoterias* species could be divided into two groups based on this feature.

The two groups also differ in the degree to which the mandibular shafts are bent ventrad approximately at the position of the penultimate tooth. In *Myrmoterias* the mandibles are strongly bent, so that there is a distinct angle visible in lateral view. *Myagroteras* ants have only a very slight bend or downward curvature at the same position.

The behavior of *Myagroteras* species has not been studied. However, it seems reasonable to assume that the presence or absence of trigger hairs must bear directly on differences in foraging behavior between the two groups, and therefore probably is a reflection of significant ecological differences. This, and the ease with which the two groups can be distinguished, suggests that formal division of the genus would be of heuristic value. A cladistic study of *Myrmoterias* with the aid of the program PAUP (version 2.3), written by David L. Swofford, has clarified the phylogeny of the genus and allowed for an evaluation of whether such a division is justified. This study suggests, but does not unequivocally support, formal division of *Myrmoterias*. Monophyly of both groups is supported if it is assumed that loss of palpal segments and of a well-demarcated frontal area is more probable than regain.

CHARACTER CODING FOR COMPUTER ANALYSIS

The characters used in the analysis are given in Table 1. Definitions of all characters are given in the section on terminology. Characters 19 and 21 (cephalic sculpture and occipital lobe sculpture) were treated as unordered; all other characters were binary or ordered. The characters were allowed free reversibility as in Wagner parsimony (Felsenstein, 1982; Farris, 1970). As discussed below, however, losses were considered more probable than gains for certain characters, a



Figures 1-2. Live workers of the genus *Myrmoteras*. 1. *M. toro* paratype (subgenus *Myagroteras*). 2. *M. barbouri* forager from Singapore (subgenus *Myrmoteras*; trigger hairs barely discernible).

TABLE 1. DATA MATRIX OF MORPHOLOGICAL CHARACTERISTICS FOR SPECIES OF MYRMOTERAS AND ONE HYPOTHETICAL OUTGROUP.†

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Outgroup	0	0	0	0	?	?	?	?	?	?	0	0	?	?	0	0	?	?
<i>M. barbouri</i>	1	1	0	0	0	0	0	P	0	0	P	1	1	0	0	1	0	0
<i>M. binghami</i>	1	1	0	0	0	0	0	1	0	P	0	0	0	0	P	0	0	0
<i>M. iridodum</i>	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
<i>M. mjoebergi</i>	1	1	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	0
<i>M. brachygnathum</i>	1	1	0	0	0	0	0	0	0	1	2	1	0	1	1	P	0	P
<i>M. ceylonicum</i>	1	1	0	0	0	0	0	0	0	1	0	0	0	1	P	P	0	P
<i>M. scabrum</i>	1	1	0	0	0	0	0	0	0	1	2	2	P	P	0	P	0	P
<i>M. bakeri</i>	0	0	1	1	1	P	1	0	0	1	1	1	1	1	1	1	0	1
<i>M. diastematum</i>	0	0	1	1	P	1	1	0	P	1	1	0-1	1	1	1	1	0	1
<i>M. indicum</i>	0	0	1	1	1	0	1	P	1	1	2-3	1	1	1	P	1	0	P
<i>M. chondrogastrium</i>	0	0	1	1	1	P	1	0	1	1	1	1	0	1	1	1	0	P
<i>M. donisthorpei</i>	0	0	1	1	P	0	1	0	0	1	1	0-1	1	1	P	P	0	P
<i>M. karnyi</i>	0	0	1	1	?	?	1	1	0	?	?	?	1	1	?	?	0	?
<i>M. insulcatum</i>	0	0	0	1	1	1	2	0	0	1	3	1	0	0	P	P	0	1
<i>M. morowali</i>	0	0	1	1	1	1	1	0	0	1	0	0	1	1	0	P	1	P
<i>M. toro</i>	0	0	1	1	P	0	1	0	0	1	0	0	1	1	P	P	1	P
<i>M. williamsi</i>	0	0	1	1	1	0	1	0	0	1	0	0	1	P	P	P	1	P
<i>M. wolasi</i>	0	0	1	1	1	0	1	0	0	1	0	0	1	1	0	P	1	P
Sg. Myrmoteras	1	1	0	0	0	?	?	0	0	?	?	0	0	?	?	0	0	0
Donisthorpei-group	0	0	1	1	1	0	1	?	?	1	1	0	1	1	?	1	0	?
Williamsi-group	0	0	1	1	1	0	1	0	0	1	0	0	1	1	0	?	1	?

† In the table "?" refers to missing data and "P" refers to a polymorphic condition, or an intermediate or ambiguous condition, as discussed in the text. Character numbers refer to the following characters: 1. trigger hairs; 2. labrum shape; 3. frontal sulcus; 4. apical mandibular bend; 5. mandibular angle; 6. mandibular grooves; 7. tooth counts; 8. preapical denticle number; 9. apical denticle number; 10. apical denticle size; 11. maxillary palps; 12. labral palps; 13. lateral clypeal flanges; 14. clypeal convexity; 15. frontal area; 16. orbital grooves; 17. postocular distance; 18. rugae above antennal bases; 19. cephalic sculpture (unordered character); 20. clypeal sculpture; 21. occipital lobe sculpture (unordered character); 22. metathoracic tubercle ruga; 23. propodeal shape; 24. metanotal groove; 25. iridescence; 26. petiolar rugae; 27. density of pilosity; 28. height of pilosity; 29. metathoracic tubercle hairs; 30. sternum of petiole; 31. propodeal declivity; 32. HW, character 1; 33. HW, character 2; 34. CI; 35. ML, character 1; 36. ML, character 2; 37. SI; 38. EI; 39. OLI; 40. TWI; 41. HFL. The final three rows of data in the table are characters for the hypothetical ancestral species of the subgenus *Myrmoteras* and the *donisthorpei* and *williamsi* species groups.

possibility not allowed for in the PAUP program.

When a character showed polymorphism within a species (i.e., the presence of mandible grooves in *M. bakeri*) it was coded as if the data were missing for that species. Species represented by single specimens were treated as polymorphic for a character if the specimen showed a borderline condition. Range limits for numerical characters were chosen to separate cleanly the maximum number of species. For several of the numerical characters (SI, HFL, TWI), species showing any overlap with the range in values be-

tween an upper and a lower limit were coded as if the data were missing; only those consistently higher than the upper limit or lower than the lower limit were assigned character states. As a result, only species demonstrating extreme differences in these characters were contrasted. This was done because the limited material available for most species is certainly not sufficient to show much of the intra-specific variation actually present. Finally, for certain characters (ocular groove, rugae above antennal bases, mandibular angle, frontal area, propodeal shape) in which the character states were judged

TABLE 1. EXTENDED.

Character																						
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?
1	0	0	0	P	P	1	0	0	1	0	0	1	1	P	1	1	0	1	P	1	P	1
3	1	0	0	P	0	1	0	P	1	0	0	1	1	1	1	1	0	1	1	1	P	1
2	1	0	P	0	0	1	0	P	1	0	0	1	1	1	1	1	P	1	1	1	0	1
2	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	1
2	1	0	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	P
1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	P
0	1	1	0	P	0	0	1	0	0	0	0	0	0	1	1	0	0	P	0	0	0	1
2	1	0	0	0	P	0	0	0	1	0	0	1	0	0	1	1	1	P	1	P	1	0
2	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	1	1	1	P	0	P
2	1	0	1	1	1	0	0	0	1	P	0	1	P	0	1	1	P	P	P	P	0	P
1	0	0	1	0	1	0	0	0	1	0	1	1	1	0	1	1	1	1	1	P	0	P
1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	1	1	1	P	1	P	1	0
?	?	?	?	1	?	?	?	?	?	?	1	?	?	?	0	1	?	?	?	1	?	?
2	1	0	P	P	P	0	0	P	1	0	0	1	1	0	1	1	1	P	0	0	P	P
1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	P	P	P	0	P	0
0	1	2	0	P	0	0	0	1	1	0	0	1	1	0	1	1	1	P	0	1	P	P
1	0	1	0	1	1	0	0	0	1	P	0	1	1	0	1	1	1	P	0	P	P	P
0	0	2	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	P	1	P	P	P
1	1	0	0	0	0	?	0	0	1	?	0	1	1	0	?	?	0	?	1	?	?	1
0	0	0	1	?	1	0	0	0	1	0	1	1	?	0	1	1	1	1	1	?	?	0
0	0	1	0	?	?	0	0	?	1	0	0	1	?	0	1	1	1	?	0	?	?	0

qualitatively, species in which there was an intermediate condition were treated as if the data were missing, because of difficulties in consistently assigning character states.

OUTGROUPS

The genus most closely related to *Myrmoteras* appears to be *Gesomyrmex* (specimens of *Santschiella*, an African genus possibly close to tropical Asian *Gesomyrmex*, were not available for study). *Gesomyrmex* females have very large eyes (in minors EI ranges from 79 to 93), and the shape of the eyes is similar to that of *Myrmoteras*. In addition, the petioles of most *Gesomyrmex* minors have a pair of ventral hairs at the base of both the anterior and posterior peduncles, as is the case with *Myrmoteras*. Monophyly of *Gesomyrmex* is evidenced by the position of the antennal bases, the eight-merous antennae, and other characters.

The mandibles of *Gesomyrmex* minors come closest within the Formicinae to re-

sembling those of *Myrmoteras* females. The mandibles are long (MI 49 to 54, or greater if the forward projection of the clypeus is excluded), and, unlike other Formicinae outside of *Myrmoteras*, the toothed margin of the mandible runs virtually parallel with the lateral margins (so that the blade is linear rather than subtriangular). Moreover, the two teeth proximal to the apical tooth are shorter than the teeth to either side of them, and in many cases are reduced in size to a degree almost comparable to the apical denticles of *Myrmoteras* (some specimens of Australian genus *Myrmecorhynchus* also approach this condition). In addition, most *Gesomyrmex* minors have the mandibles relatively strongly curved ventrad at about the same position as the strong apical mandible bend characteristic of the subgenus *Myrmoteras*. Thus, the mandibles of many *Gesomyrmex* minors seem to be approaching the condition characteristic of *Myrmoteras*.

The proventriculus of *Gesomyrmex* is

sepalous, which is the derived condition for Formicinae (Eisner, 1957). In contrast, the proventriculus of *Myrmoteras* lacks sepals. The anatomy of the *Myrmoteras* proventriculus is unusual, however, and not well understood (Eisner, 1957). The asepalous condition of the proventriculus in *Myrmoteras* does not preclude a close relationship to *Gesomyrmex*, although further comparative studies using proventricular structure and other characters will be necessary to clarify the phylogenetic relationships of these and other formicine genera.

CHARACTER POLARITY

Comparison of *Myrmoteras* with *Gesomyrmex*, *Myrmecorhynchus*, and other Formicinae indicates that several characters found to vary within *Myrmoteras* can be polarized for cladistic analysis. *Gesomyrmex* and *Myrmecorhynchus* show at most a trace of the frontal sulcus; the presence of a well-defined sulcus is therefore considered synapomorphic within the genus *Myrmoteras*, as is the lack of a distinct apical mandible bend.

In all other formicines examined the labrum either lacks a distinct dorsalmost surface, or this surface is narrow and truncate. In genera such as *Gigantiops*, *Opisthopsis*, *Camponotus*, and *Formica* the (often numerous) labral hairs are short to moderately long (but apparently never longer than the length of the labrum; see Gotwald, 1969). By contrast, in the genera *Oecophylla* (Gotwald, 1973), *Myrmecorhynchus*, and *Gesomyrmex* the labrum has one or two pairs of hairs which are much longer than any other labral pilosity. These hairs are very slender and originate far apart on the labrum, and thus resemble those of *Myagrotas*. The hairs either project back over the mouthparts, or more or less forwards, beneath the mandibles. In *Gesomyrmex* there is often only a single pair of long, widely separated hairs, and in some species these hairs are almost as long as the mandibles. These observations support the view that the

trigger hairs and projecting labrum of species in subgenus *Myrmoteras* represent synapomorphies.

Well-developed ocular grooves, the presence of a slight iridescent sheen, and the strongly dilated condition of the middle and hind tibiae are characters apparently unique to certain species of this genus, and these character states are therefore considered synapomorphies. The 6,4 palpal formula and presence of a well-defined frontal area were treated as plesiomorphies.

CLADISTIC ANALYSIS

In the initial runs of the complete data set I used global branch swapping with MULPARS (search for multiple minimum length trees). Unfortunately, the PAUP program does not allow for irreversible conditions: I consider the loss of palpal segments and complete loss of a well-demarcated frontal area to be much more probable than regain. The initial run resulted in trees where reversals in the loss of these characters occurred. At this point an attempt was made to find more parsimonious trees by reducing the likelihood of reversals.

Several of the reversals present in the trees from the initial run occurred within clusters of species. These species clusters consistently resolved regardless of whether palpal and frontal area characters were used in the analysis; there were also characters supporting the monophyly of each of these clusters. Therefore, each cluster was collapsed to a single, hypothetical ancestor species, with the assumption that any of the tree configurations found during runs with or without palpal and frontal area characters could represent the actual phylogeny of the cluster. The clusters involved were the *ceylonicum* and *binghami* species groups, which were further collapsed to a single taxon, and the *donisthorpei* group; this reduced the number of taxa to ten. The character states assigned to the ancestral species for each group were deduced through consider-

ations of parsimony using the algorithm of Maddison *et al.* (1984), except for the following characters: maxillary palpal segmentation, labral palpal segmentation, and frontal area. Since losses for these characters are considered essentially irreversible, the highest number of palpal segments and best-developed condition of the frontal area within each group were treated as the ancestral condition for that group.

The *williamsi* group was consistently resolved in the six most parsimonious trees found for this modified data set. The number of taxa under consideration could then be further reduced by collapsing the *williamsi* group to a single ancestral taxon. With the number of taxa reduced to seven it became possible to carry out an exhaustive search for the most parsimonious trees. The three resulting trees are given in Figure 3 (trees A–C), along with the basic structure of the majority of trees from the initial run (tree D).

RESULTS

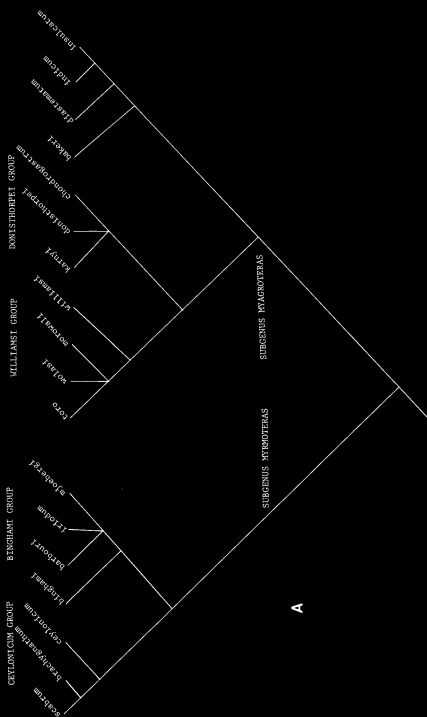
Inclusion of the complete data matrix consistently results in the placement of the subgenus *Myrmoter* as the sister group to the species *M. insulcatum* within the *Myagroteras* tree. However, when the initial data set is considered without palpal and frontal area characters, *Myrmoter* and *Myagroteras* resolve as monophyletic sister taxa. Monophyly of both groups is also realized when the occurrence of regains in palpal and frontal area characters is constrained by first collapsing species groups as discussed in the previous section. The three trees resulting from this procedure contain 101 steps (including changes within the collapsed groups), five more than the most parsimonious trees found when no restrictions were made on reversals in palpal segment and frontal area loss. Of these, tree A (Fig. 3) is considered most reasonable because it assumes one event of palpal segment and frontal area regain, rather than two. I have chosen to accept this tree, and therefore

the monophyly of both groups, because trees in which the subgenus *Myagroteras* is paraphyletic (for example, Fig. 3, tree D) are less parsimonious given my initial assumptions on character evolution. This is true even after the number of reversals in the palpal and frontal area characters is reduced by manually recoding transitions between character states on these trees. Monophyly of *Myagroteras* is supported by the frontal sulcus and mandibular bend characters (although the results do not change if the mandibular bend character is not polarized). (Monophyly of *Myrmoter* is supported by the labral shape and pilosity [trigger hair] characters.)

In the subgenus *Myrmoter*, the *ceylonicum* and *binghami* groups consistently resolved as monophyletic sister groups. *M. ceylonicum* is the sister taxon to the other species in the *ceylonicum* group. *M. barbouri*, *iriodum*, and *mjoebergi* form a clade within the *binghami* group, although the relationship between these species is unclear.

The structure of the *Myagroteras* tree is less certain. The species *M. williamsi* is most likely the sister taxon to other species in the *williamsi* group, but if palpal segment characters are deleted from consideration, the species sorts out at the base of the *donisthorpei* clade near *M. karnyi*. Although the *donisthorpei* group was consistently resolved as monophyletic, placement of *M. karnyi* in this group is problematic because the type (and only known specimen) of this species was not located. The possibility remains that *M. karnyi* is actually closer to *M. williamsi*. Placement of *M. karnyi* in the *donisthorpei* group was a result of coding for probable similarities in petiolar shape and sculpture based on the original description (Gregg, 1954).

The position of the species *M. insulcatum* in the tree is unclear. This ant represents either the sister taxon to other *Myagroteras* species (as in Fig. 3, tree C), or is derived from the *M. bakeri* group (Fig.



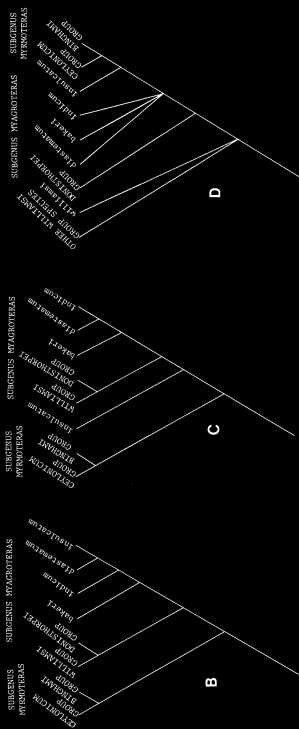


Figure 3. Alternate cladograms of the genus *Myrmoteras*. Trees A-C result from the assumption that reversal of palpal segment or frontal area loss is unlikely (see text for methods used). Tree D shows the structure common to most of the equally parsimonious trees obtained when loss and gain of the same characters were treated as equally likely. Nodes with more than two branches indicate unresolved relationships. Only tree A is presented in its entirety; in the other trees the positions of monophyletic species groups are indicated.

3, trees A and B). Given the latter hypothesis, and presuming *Myagroteras* is monophyletic, the character states this species uniquely shares with subgenus *Myrmoteras* (such as in clypeal shape and lack of the frontal sulcus) must represent homoplasies.

The adequacy of the phylogeny supported here will become clearer when additional material from the genus is available, as future collections of *Myrmoteras* will certainly continue to yield a high proportion of new species, and should also greatly clarify intraspecific variation.

TERMINOLOGY AND CHARACTER STATES

Below I define the measurements, indices, and special descriptive terms used in this revision. In cases where the character in question was used in the cladistic analysis, the individual character states are also defined, with the coding for each state used in cladistic analysis given in brackets. Unless otherwise indicated, the characters were treated as an ordered sequence of states. Character states coded as [?] were treated as absent data (see previous section).

Precise measurements are necessary to determine subtle differences in body proportions that often distinguish species. Measurements were made with an ocular micrometer on a Leitz microscope, to a precision of at least 0.01 mm, except measurements of trunk length, which are precise to an estimated 0.03 mm. All measurements are given to the nearest 0.01 mm; indices such as CI were calculated before converting micrometer units to millimeters. Sculpturing terminology follows that of Harris (1979). Scanning electron micrographs were prepared with an AMR 1000a SEM, using gold-palladium coated specimens.

GENERAL CHARACTERS

Iridescence. Refers to presence of a fine iridescent sheen on the head and trunk.

Character states: [0] no iridescence (al-

though body surface often lustrous); or [1] feebly iridescent.

Pilosity. Generally refers to the long, conspicuous erect to suberect hairs on the head and body.

Height. Typical height of longer hairs on trunk. **Character states:** hairs [0] long (height at least 0.18 mm); or [1] short (height < 0.15 mm).

Density. Estimated for workers by counting hairs breaking dorsal margin of trunk viewed in profile, excluding hairs arising from metathoracic tubercles. **Character states:** pilosity [0] sparse (less than 10 hairs) to moderate (10 to 29 hairs); or [1] dense (30 to 39 hairs) to very dense (40 hairs or more).

TL (Total length). Sum of ML + HL + WL + petiole length + gaster length. Sizes small (less than 5.0 mm), medium (5.0 to 6.0 mm), or large (greater than 6.0 mm).

CHARACTERS ON HEAD (EXCLUDING MANDIBLES)

CI (Cephalic index). $100 \times \text{HW/HL}$. **Character states:** head [0] narrow (CI at most 108); or [1] broad (CI > 108).

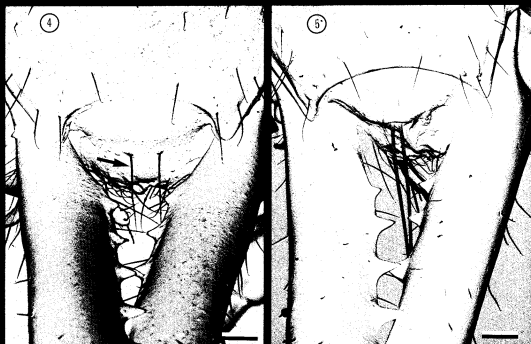
Cephalic sculpture. **Character states** (unordered character): dorsum of head (excluding clypeus) is [0] conspicuously rugose; [1] granulate; [2] smooth (excluding fine, feeble rugae between antennal bases); or [3] punctate.

Clypeal sculpture. **Character states:** clypeus [0] granulate or granulo-rugose; or [1] lacking granulate sculpture.

Clypeus, convexity. **Character states:** clypeus [0] feebly convex medially; [?] intermediate condition; or [1] strongly convex medially.

Clypeus, lateral flanges. **Character states:** lateral flanges [0] relatively poorly defined; [?] intermediate condition; or [1] well-defined because of relatively abrupt shift in plane relative to raised medial region.

EI (Eye index). $100 \times \text{EL/HW}$. **Charac-**



Figures 4–5. Labral structure in an oblique anterior-dorsal view. 4, Labrum of *M. indicum* (subgenus *Myagroteras*); the arrow indicates one of the long labral hairs. 5, Labrum of *M. mjoeborgi* (subgenus *Myrmoteras*).

Scale lines, 0.05 mm.

ter states: [0] EI at most 60; or [1] EI > 60.

EL (Eye length). The maximum diameter of the eye.

Full face. Dorsal surface of head viewed so as to attain the maximum length.

Frontal area. Character states: [0] clearly defined; [?] poorly demarcated (by subtle color differences, very feeble or incomplete sutures, or both); or [1] not demarcated.

Frontal sulcus. Sulcus on head extending from frontal area to median ocellus.

Character states: [0] absent or very feeble (usually visible as a trace of an impressed line, e.g., Figs. 11–14, 33); or [1] conspicuous (e.g., Figs. 27, 38).

HL (Head length). Length of head along midline from anterior margin of clypeus to posterior margin of medial portion of the occipital lobe, measured with the head viewed in full face.

HW (Head width). Maximum width of head viewed in dorsal full-face, excluding the eyes. Preferred over total length as an index of size. **Character 1, states:** size [0] small (HW 0.90 mm or less); or [1] intermediate to large (greater than 0.90 mm). **Character 2, states:** size [0] small to intermediate (HW less than 1.10 mm); or [1] large (1.10 mm or more).

Labrum shape. Character states: in full face view visible (dorsal) part of labrum [0] rounded or truncate (projecting very little; e.g., Figs. 4, 27); or [1] triangular to subtriangular (projecting more conspicuously and coming to a forward point; e.g., Figs. 5, 14).

Occipital lobe. A conspicuous lobe shaped somewhat like an inverted “V” situated immediately above and to the sides of the foramen magnum. The lobe is narrowest above foramen and is most

prominent on either side of head (e.g., Figs. 7-9).

OLI (Occipital lobe index). The proportion of the head length measurement accounted for by the median portion of the occipital lobe, multiplied by 100. **Character states:** [0] less than 10; or [1] 10 or more.

Occipital lobe sculpture. Character states: (unordered character): lobe [0] smooth; [1] granulate; or [2] rugose.

Orbital grooves. Narrow sulci along the dorsal border of each eye. **Character states:** [0] virtually absent (at most a very narrow, feeble groove; e.g., Figs. 11-14); [?] moderately developed (narrow but readily discernible groove, often with feeble transverse rugae); or [1] conspicuous (groove wider, usually with well-developed transverse rugae; e.g., Figs. 26, 27).

Palpal segmentation. Given in species descriptions as number of segments in maxillary palps; number of segments in labial palps. Because of the limited material counts were made on undissected individuals, when necessary after applying a droplet of relaxing fluid to the mouthparts.

Labial palps. Character states: labial palp segments numbering [0] four; [1] three; or [2] two.

Maxillary palps. Character states: maxillary palp segments numbering [0] six; [1] five; [2] four; or [3] three.

Postocular distance. The distance between the posterior margin of the eye and the abrupt posterior declivity of the head behind the eye, measured in dorsal full face view (Fig. 38). **Character states:** distance [0] narrow (less than 20% of eye length); or [1] wide (at least 20% of eye length).

Rugae above antennal bases. Narrow rugae curving above antennal fossae, apparently as an extension of the raised borders of the fossae. **Character states:** [0] essentially absent (very short and feeble, or absent); [?] moderately developed (longer, less feeble rugae); [1] con-

spicuous (rugae well developed, e.g., Figs. 26, 27).

SI (Scape index). $100 \times SL/HW$. **Character states:** [0] 100 or less; [?] intermediate; or [1] 110 or more.

SL (Scape length). The maximum length of the scape, excluding the basal radicle.

Trigger hairs. Character states: [0] absent, although with two relatively short, slender hairs originating well apart and somewhat ventrad on labrum (Fig. 4), or even more widely separated (in *M. insulcatum*, Fig. 37); or [1] present (two long, thickened hairs originate from adjacent points medially on dorsal surface of labrum; Fig. 5).

CHARACTERS ON MANDIBLES

Apical denticles. Relatively very small teeth between the apical and penultimate teeth.

Number. Character states: apical denticles numbering [0] two; or [1] one.

Size. Character states: longest (most distal) of the apical denticles [0] large (length more than 18% of that of the apical tooth, measuring both from the crotch between them); or [1] small (less than 18%).

Angle, mandibular. Feeble inward bend at a point along outer margin of shafts at about a third the distance from mandible bases to the apical tooth. **Character states:** angle [0] absent (e.g., Fig. 11); or [1] present (Fig. 27).

Apical mandibular bend. In all species the mandible shafts curve gently downwards throughout their lengths when viewed from the side. In addition, however, the shafts are more or less distinctly bent ventrad at about the position of the penultimate tooth. When the bend is strong the apical tooth is conspicuously below the plane of the adjacent teeth. **Character states:** apical bend [0] strong (bend ca. $> 35^\circ$; Fig. 6A); or [1] feeble (bend or curve of ca. $< 20^\circ$; Fig. 6B).

Grooves, mandibular. A single, feeble

groove extending longitudinally along the dorsal surface of the shaft of each mandible. **Character states:** [0] absent; [?] very feeble and extending less than half the length of the mandible shafts; [1] present and extending most of the length of mandibular shafts, and positioned either very close to the toothed inner margin of the mandible (character apparently unique to *M. insulcatum*, Figs. 33, 37), or down the middle of the shaft (e.g., Fig. 38).

MI (Mandible index). $100 \times \text{ML}/\text{HL}$. (For character states see ML [Mandible length].)

ML (Mandible length). Measured from the tip of the apical mandibular tooth to the lateral clypeal tooth on the same side as the mandible being measured, with the mandible extending ahead (closed); the measurement was taken with the basal length of the mandible shaft perpendicular to the angle of view. **Character 1, states:** mandible length [0] significantly less than head length ($\text{MI} < 95$); or [1] longer. **Character 2, states:** mandible length [0] longer than head but significantly shorter than trunk ($\text{ML}/\text{WL} < 95$); or [1] longer. Queens often have slightly shorter mandibles relative to WL, and so data for queens were not used for character 2 (other than that for the holotype of *M. insulcatum*, which shows state [1]).

Preapical denticles. Denticles (defined as any tooth less than 60% the length of the teeth on either side of it) occurring between teeth proximad to the penultimate tooth. **Character states:** numbering [0] one or more; or [1] entirely absent.

Tooth counts. Counts of the teeth on the mandibles can be useful for species identification, although species do not have a constant number of teeth, as seems to have been assumed previously (indeed, counts for the left and right mandibles of the same specimen often differ by one or two teeth; I therefore generally examined both mandibles).

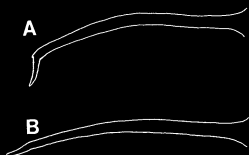


Figure 6. Mandible bend character. Mandibles drawn in lateral view. A. Typical condition in *Myrmoteras*. B. Typical condition in *Myagrotomas*.

Mandibular tooth counts exclude preapical and apical denticles (*q.v.*), although since teeth steadily decrease in size basad, the proximal teeth are often smaller than some denticles. **Character states:** mandibles with [0] 8 to 9 teeth; [1] 10 to 13 teeth; or [2] 14 teeth or more (in *M. insulcatum*).

CHARACTERS ON TRUNK, PETIOLE, AND LEGS

HFL (Hind femur length). The maximum length of the hind femur. **Character states:** Value for $100 \times \text{HFL}/\text{HL}$ is [0] 110 or less; [?] intermediate; or [1] 120 or more.

Metanotal groove. When the trunk of a worker is viewed in profile, the position of the metanotal groove is often indicated by a notch. **Character states:** metanotal groove is [0] conspicuously impressed (referring specifically to the presence of a narrow, well-defined notch; Fig. 42); or [1] poorly defined or absent (e.g., Figs. 7, 18).

Metathoracic tubercles. Conspicuous tubercles in workers, on which are located the metathoracic spiracles (Figs. 7, 8).

Metathoracic tubercle pilosity. Prominent hairs rising on or very near the base of each tubercle (workers only). **Character states:** Hairs at each tubercle numbering [0] at least two; or [1] at most one.

Metathoracic tubercle ruga. Ruga clearly

originating immediately anterior to the base of each metathoracic tubercle, which extends forward across mesothorax along dorsolateral margin (found in workers only). **Character states:** Rugae [0] absent; or [1] present (Figs. 7, 8).

Petiolar rugae. With feeble rugae extending transversely across anterior and posterior apices of node summit. **Character states:** rugae [0] absent (summit of node smooth, usually rounded); or [1] present.

Propodeal declivity. **Character states:** declivity of propodeum [0] transversely rugose; or [1] rugae lacking.

Propodeal shape. **Character states:** in workers, dorsum of propodeum [0] flat (e.g., Fig. 45); [?] slightly convex (e.g., Fig. 43); or [1] strongly convex (e.g., Figs. 7, 44).

Sternum of petiole. **Character states:** in profile the portion of the ventral margin of petiole lying directly beneath the node is [0] virtually straight, feebly convex, or feebly concave; or [1] conspicuously convex (e.g., Fig. 34).

TWI (Tibial width index). $100 \times$ the maximum width of the middle tibiae in lateral view divided by their maximum length. **Character states:** middle tibiae [0] relatively thin ($TWI < 21$); [?] moderately dilated (TWI intermediate); or [1] strongly dilated ($TWI > 23$).

WL (Trunk length). Distance from the posteriormost point ventrad on the propodeum to the anterodorsal slope of the pronotum, measured with the trunk in profile. Since the pronotum gently curves forward into the cervix, the measurement was taken from the point along the slope where a line tangent to the slope would form an angle of about 45° upon intersecting the plane of the cervix.

LOCALITY DATA AND REFERENCE COLLECTIONS

Locality data for each series conclude with the number of individuals of each caste examined by the author and (in parentheses) the collector(s) of the series, and the museum(s) in which the material is

deposited. The latter are designated by the abbreviations that follow: British Museum (Natural History), London (BMNH); Museo Civico di Storia Naturale, Genoa (MCSN); Museum d'Histoire Naturelle, Geneva (MHN); and Museum of Comparative Zoology, Harvard University, Cambridge (MCZ).

Myrmoteras

Myrmoteras Forel, 1893: 607. Type species *Myrmoteras binghami* Forel by monotypy.

Diagnosis. Formicine ants with a distinctive transverse occipital lobe present in all castes. Female castes very similar in appearance, with very large heads; huge, convex eyes; and very long, linear mandibles with well-developed teeth. Males with heads small relative to females; eyes large, convex; scapes long, SI values within range of females; mandibles greatly reduced and without teeth.

Worker. Small to moderately sized (TL 3.9 to 7.0 mm) monomorphic ants belonging to the subfamily Formicinae. Head very large, broader than trunk or gaster, and at least half as long as trunk. Head strongly constricted in back of ocelli so as to form a clearly demarcated occipital lobe which extends transversely across the back of the head; the lobe is narrowed medially above the foramen magnum. Eyes huge, oval and strongly convex, well over half as long as the head length; taking up most of lateral surfaces of head. Ocelli invariably present. A hair originating beneath each compound eye projects forward to either side of clypeus and is usually visible in full face view. Antennae 12-merous; scapes long, gently curved and incrassate distad, invariably extending well beyond occiput; funiculus with segments III generally shortest, terminal segment the longest by far. Antennal fossae positioned dorsally between eyes rather than anterior to eyes as in *Gesomyrmex*; insertions far apart near eye margins and some distance behind the clypeus. Frontal carinae absent, although margins of antennal fossae somewhat raised.

Mandibles slender and extremely elongate, usually longer than head (at minimum 85% as long as head), with the toothed margin running virtually parallel with lateral margins (never subtriangular as in most formicines); somewhat wider than deep in cross section. Mandibular teeth well separated, numbering 8 to 14. The proximal teeth are tiny, but distally the teeth become longer, slender and sharp. There are invariably one or (more commonly) two apical denticles between the apical and penultimate teeth. Mandibles articulated laterally, not relatively close together along anterior margin as in *Odontomachus* (where the front of the head is strongly constricted); nevertheless, the mandibular bases are more approximate than in other formicines because the front of the head is relatively narrow. Clypeus about 25 to 50% wider than long, lacking a feeble medial ridge; generally having a well-developed clypeal tooth at each forward corner and with more or less conspicuous lateral flanges. Clypeus not conspicuously produced, leaving mandible bases and labrum exposed. Labrum elongate, with a small, dorsalmost portion visible in full face view; the remainder projects downward between mandible bases. Palpal formula variable: maxillary 3 to 6; labial 2 to 4 segments.

Trunk (Figs. 7, 8) elongate, widest at pronotum, and somewhat dumbbell-shaped, as the mesothorax is constricted and narrow, with its dorsal and ventral surfaces virtually straight and parallel in profile; pronotum and propodeum relatively massive, convex to flattened above. Metathoracic spiracles raised on conspicuous tubercles. Petiole with prominent peduncles; node broad in front view (usually widest near crown), thick and more or less rounded in profile; never strongly anteroposteriorly compressed. Sternum of petiole virtually without hairs except for a pair of ventrolaterally placed hairs near the base of each peduncle (e.g., Fig. 29). Gaster rounded, with a prominent circlet of hairs around the acicopore; about the size of the head or smaller. Legs long, with

tibiae distinctly thicker than femora; middle and hind tibiae often conspicuously dilated.

Queen. Virtually identical to workers in size (including WL and gaster size), proportions and morphology, but alate. Trunk (Fig. 36) high and convex, having a full complement of flight sclerites, and often sculptured somewhat differently than in the worker.

Male. Known only for subgenus *Myrmoteras*. Head small relative to females (Fig. 9), widest immediately behind eyes. Occipital lobe present, well developed. Eyes very large and convex, but relatively smaller than in workers (about half as long as head length); ocelli conspicuous. Antennae 13-merous; relative to head size scape about as long as in females; funiculus long and filiform. Mandibles greatly reduced and edentate, subtriangular with blunt tips; barely extending forward of labrum when opened and not capable of meeting apically at full closure. Forward margin of clypeus rounded, lacking teeth. Palpal segmentation variable as in females.

Trunk (Fig. 10) similar to that of queen. Node of petiole broader than in females; pairs of ventrolateral hairs near bases of peduncles present. Middle and hind tibiae slender relative to females, about as thick as femora. Parameres simple in outline, with narrow, blunt tips and having numerous setae. Pygostyles present. Digitus of volsella heavily sclerotized and strongly curved downwards, coming to a sharp terminal point, and finely serrate along dorsal margin; cuspidal lobes small, rounded. Aedeagus a pair of broad subrectangular plates. (Description of male genitalia based largely on *M. indicum*.)

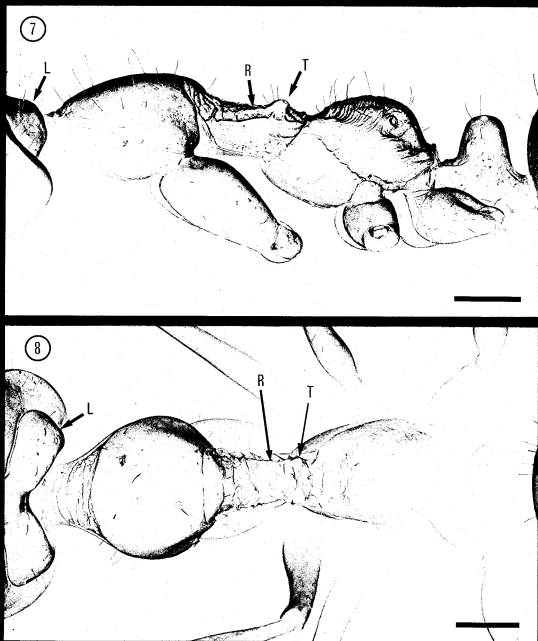
Fore wings with Mf1 present, and with Rs + M present but somewhat contracted (Brown and Nutting, 1949).

SYNONYMIC LIST OF SPECIES

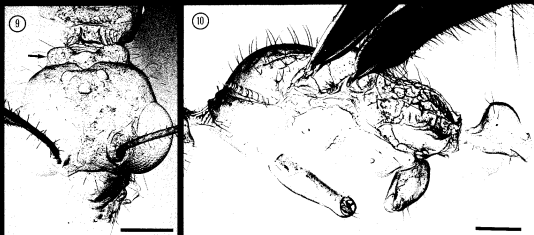
Subgenus *Myrmoteras* Forel, 1893.

binghami-group.

barbouri Creighton, 1930. Java, Peninsular Malaysia, Sabah, Sarawak.
= *kemneri* Wheeler, 1933.



Figures 7-8. Trunk of a *Myrmoteras indicum* worker (series 58 of Besuchet and Löbl). T - metathoracic tubercle; R = metathoracic tubercle ruga; L = occipital lobe. 7. Lateral view. 8. Dorsal view.
Scale lines. 0.25 mm.



Figures 9-10. Male of *Myrmoterias indicum* (series 58 of Besuchet and Löbl). 9. Head (arrow indicates occipital lobe). 10. Trunk.

Scale lines, 0.25 mm.

- binghami* Forel, 1893. Burma, Thailand.
tridum sp. nov. Kalimantan, Sarawak, Peninsular Malaysia.
mjoebergi Wheeler (in Creighton, 1930). Borneo (Sarawak?).
ceylonicum-group.
brachygnathum sp. nov. Southern India.
ceylonicum Gregg, 1956. Sri Lanka.
scabrum sp. nov. Southern India.
 Subgenus *Myagroteras* new subgenus.
bakeri-group.
bakeri Wheeler, 1919. Sabah, Peninsular Malaysia.
diastematum sp. nov. Sarawak.
indicum sp. nov. Southern India.
donisthorpet-group.
chondrogastrum sp. nov. Sarawak.
donisthorpet Wheeler, 1916. Sarawak, Sabah, Kalimantan.
karnyi Gregg, 1954. Mentawai Archipelago.
insulcatum-group.
insulcatum sp. nov. Philippines (Luzon).
williamsi-group.
morowali sp. nov. Sulawesi.
toro sp. nov. Sulawesi.
williamsi Wheeler, 1919. Philippines.
wolast sp. nov. Sulawesi.

KEY TO MYRMOTERAS WORKERS AND QUEENS

The workers and queens of those *Myrmoterias* species in which both castes have been described are very similar except for characters on the trunk. In the key that follows I make the assumption that this

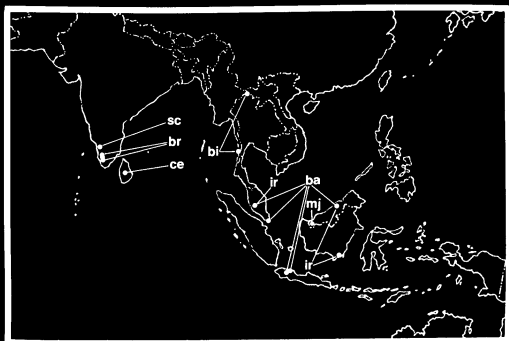
holds true for species in which one or the other caste remains undescribed.

1. A pair of long trigger hairs originates from middle of labrum; surface of labrum visible in full face view conspicuously projecting, more or less triangular (Fig. 5); frontal sulcus very feeble or absent (subgenus *Myrmoterias*) 2
- Without trigger hairs; surface of labrum visible in full face view rounded or truncated, not strongly projecting (Fig. 4); frontal sulcus on head usually prominent (subgenus *Myagroteras*) 8
- 2 (1). Mandibles longer than head (MI > 110); cephalic index < 105; from Southeast Asia (*binghami* group) 3
- Mandibles as long as head or shorter (MI < 105); head wider (cephalic index > 105); from India (*ceylonicum* group) 6
- 3 (2). In addition to scattered long hairs, pronotum and dorsum of head with numerous very short, fine hairs, and smooth with minute shallow punctures; mandibles lacking denticles except for apical pair *binghami*
- Without short fine pilosity on head and pronotum; sculpture not as described; with one or more denticles on mandible in addition to apical pair 4
- 4 (3). Head and pronotum distinctly granulate (Fig. 11) *barbouri*
- Head and pronotum smooth or virtually

- smooth, with at most traces of granulate sculpture 5
- 5 (4). Head and trunk shining and smooth except for very poorly defined longitudinal rugae on mesothorax in worker (Fig. 18), and with very sparse long hairs *mjoebergi*
- Head and trunk much less strongly shining, virtually smooth except for mesothorax of workers, which is more lustrous and has conspicuous narrow irregular rugae (Fig. 17); long hairs moderately numerous *triodum*
- 6 (2). Dorsum of head smooth *brachygnathum*
- Dorsum of head sculptured 7
- 7 (6). Dorsum of head strongly granulo-rugose (Fig. 21) *scabrum*
- Dorsum of head evenly granulate (Fig. 20) *ceylonicum*
- 8 (1). Dorsum of head and pronotum granulate or rugose 9
- Dorsum of head and disc of pronotum smooth (except for very feeble rugae on frons of some species) 15
- 9 (8). Head feebly sculptured; petiole strongly convex beneath node (Fig. 34); with a relatively conspicuous ruga which originates anterior to base of each metathoracic tubercle and extends forward across mesothorax (Fig. 7); maxillary palps with five segments or fewer (*donisthorpei* group) 13
- Head strongly sculptured; petiole feebly convex or concave beneath node; lacking conspicuous narrow ruga described above; maxillary palps with six segments (*williamsi* group) 10
- 10(9). Evenly granulate all over dorsal and lateral surfaces of head and trunk; in workers mesonotum greatly depressed relative to the pronotum and propodeum, which are very high and rounded (Fig. 44); from the Philippines *williamsi*
- Sculpture different from above; occiput, surface of head beneath eyes, and mesothorax without regular granulate sculpture. In workers pronotum and propodeum not strongly convex, mesonotum depressed, but not strongly so; from Sulawesi 11
- 11(10). Propodeum of worker moderately convex (Fig. 43); head and pronotum with narrow longitudinal rugae, without granulate sculpture on clypeus *toro*
- Propodeum of worker conspicuously flattened dorsally (Figs. 42, 45); clypeus granulate 12
- 12(11). Head longitudinally rugose, except for clypeus and frontal area, which are evenly granulate *wolasi*
- Head entirely granulate dorsally, except for frontal area, which is smooth and shining *morowali*
- 13(9). Gaster granulate dorsally *chondrogastrum*
- Gaster entirely smooth 14
- 14(13). In worker, propodeum and pronotum high, convex; mesonotum relatively depressed (queen not known) *karnyi*
- Worker with propodeum and pronotum not high and strongly convex, so that summit of propodeum is about level with mesonotum *donisthorpei*
- 15(8). No trace of frontal sulcus (*insulcatum* group) *insulcatum*
- Frontal sulcus conspicuous (*bakeri* group) 16
- 16(15). Wide sulcus between clypeus and head capsule (Fig. 26); shallow grooves proceed longitudinally dorsad on mandibles for most of the length of the shafts *diastematum*
- Very narrow gap between clypeus and head capsule (Fig. 27); grooves on mandibles usually absent or poorly developed 17
- 17(16). Mandible with two apical denticles, smallest tiny but readily visible; middle tibiae moderately dilated, 16 to 20% as wide as long; propodeum dorsally flattened; from the Malay Archipelago *bakeri*
- Mandible with single apical denticle; middle tibiae thick (26 to 27% as wide as long); propodeum evenly convex; from southern India *indicum*

Subgenus *Myrmoteras*

Workers and queens readily distinguished from subgenus *Myagroteras* by the presence of a pair of prominent trigger hairs. When viewed in perfect full face, the visible part of the labrum is triangular, coming to a more or less distinct forward point from which the trigger hairs originate. Although initially directed somewhat downward and between the bases of the mandibles, the hairs curve gently forward and then extend directly ahead immediately beneath the mandible shafts to 45 to 95% of the distance to the apical tooth. The hairs are much thicker than other body hairs, and are pliable, rarely breaking even in dried material. In some museum specimens the hairs are bent and widely separated. In life, however, the



Map 1. Distribution of species in the subgenus *Myrmoteras*.

Abbreviations: ba = *M. barbouri*, bi = *M. binghami*, br = *M. brachygnathum*, ce = *M. ceylonicum*, ir = *M. iriodum*, mj = *M. mjoeborgi*, sc = *M. scabrum*.

hairs are aligned very close together, if not in actual contact through their lengths (Fig. 2).

Frontal sulcus very feeble or absent, usually visible only as a slight trace of an impressed line in some lights; never conspicuous as in *Myagroteras*. Orbital grooves moderately developed to virtually absent; never conspicuous. Narrow ridges curving above antennal carinae absent or moderately developed. Frontal area usually not demarcated at all. Clypeus feebly convex over a broad median region or (in *M. brachygnathum* and *ceylonicum*) more strongly convex; but with lateral flanges somewhat less conspicuous than in *Myagroteras* because shift in plane relative to margins of the raised medial region is reduced.

Mandibles shorter than in most *Myagroteras* species, as long as trunk or

shorter ($ML/WL < 0.95$ except in some *M. iriodum* workers). The mandible shafts bend ventrad about 45° at about the position of the penultimate tooth (less strongly bent in *ceylonicum*). In dorsal view outer margins of shafts proximately virtually straight to feebly convex (becoming progressively more strongly convex distad); without a slight bend at about a third the distance to the mandible tips. Apical denticles often larger and stouter than in *Myagroteras*.

This subgenus contains seven species distributed from India and Sri Lanka to Thailand, peninsular Malaysia, Borneo and Java. Included are all of the largest species of *Myrmoteras* (species with head widths of 1.10 mm or more); however, two species in the *ceylonicum* group are relatively small. The worker is known for all species, the queen for three, and the male for none.

THE BINGHAMI GROUP

Size medium to large (TL 5.5 to 7.0 mm). Head narrower than in *ceylonicum* group (CI < 102); occipital lobe slightly thicker (OLI 10 to 13). Orbital grooves essentially absent, but the apparent remnants usually visible as extremely narrow, feebly impressed grooves dorsad along margins of eyes. Frontal area not demarcated (except in *M. binghami*, in which the frontal area is visible but ill defined). Ridges above antennal bases essentially absent. Palpal segmentation variable; known extremes 6.4 and 4.3. Mandibles longer than in *ceylonicum* group (MI > 110); number of mandible teeth usually 11 to 13 (8 to 9 in *binghami*). Apical denticles often large, sometimes pair reduced to a single denticle. Mandibles bent ventrad distally to a degree intermediate between that described for *M. ceylonicum* and *M. scabrum* in the *ceylonicum* group; that is, when viewed from above with the basal portion of the shafts perpendicular to the angle of view, the apical tooth and subapical denticles are obviously shifted out of the plane of the other teeth, but not so strongly as to be obscured by the penultimate tooth. Integument lustrous, but in addition head and trunk with a feeble to moderately conspicuous iridescent sheen (virtually lacking on mesothorax) not found in any other species in the genus.

Species in this group are known from Thailand and the Malay Archipelago. What little information is available indicates these ants inhabit moist tropical forests.

Myrmoteris barbouri

Figures 2, 11, 15; Map 1

Myrmoteris barbouri Creighton, 1930: 185, fig. 2, pl. 11, fig. 6. Java, Singdanglalia [Singdanglaja?]. 1 worker (T. Barbour, MCZ [examined]).

Myrmoteris kemneri Wheeler, 1933: 73, fig. 1. Indonesia: Java: Tjibodas [=Cibodas], May 29, 1921, 1 worker (N. A. Kemner, MCZ [not found]). PROVISIONAL NEW SYNONYMY.

Diagnosis. *M. barbouri* is readily distinguished from all other species in the

binghami group by its conspicuous granulate sculpturing.

Worker. Holotype: TL 6.7, HW 1.28, HL 1.25 (CI 102), ML 1.58 (MI 126), SL 1.56 (SI 122), EL 0.76, HFL 1.68 (TWI 21), WL 1.86 mm. Frontal sulcus very feeble, discernible only to height of antennal bases. Palpal segmentation 5.3. Mandibles with 10 teeth and one preapical denticle; apical pair of denticles on both mandibles apparently worn off or broken (not absent as has been supposed by Creighton [1930] and others). Other material of this species has mandibles with 9 to 11 teeth (usually 10) and 1 to 2 preapical denticles (usually 1). The denticle between the penultimate tooth and the one proximal to it is almost half the height of the adjacent teeth and is thus unusually prominent (much less than half the height in other species).

Pronotum slightly flattened above; propodeum evenly convex. Metanotal groove not visible as a conspicuously impressed notch in profile. Node of petiole high and massive, in side view with sloping, straight to slightly concave anterior and posterior faces and with summit narrow relative to base and somewhat flattened (moderately rounded above when viewed from the front). Ventral margin of petiole feebly convex beneath node.

Dorsal surface of head granulate, grain very even and fine (diameters ca. 0.01 to 0.02 mm), similar to *M. ceylonicum* but more delicate; clypeus medially more feebly granulate; back of head virtually smooth. Sculpture on pronotum and propodeum similar to dorsum of head but relatively feeble, particularly on sides; in some lights propodeum appearing to have very feeble transverse rugae across dorsum. Mesothorax with several weak to moderately strong oblique rugae on sides, virtually smooth, but with traces of fine longitudinal rugae dorsally. Pilosity moderately dense, with 20 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.08 mm on head and 0.13 mm on trunk and gaster. Two hairs on or near

each metathoracic tubercle, node of petiole with ca. 4 to 8 hairs. Reddish orange, with gaster and antennae yellowish orange, legs same but darker; petiole and mandibles orange.

Queen. Previously undescribed. A single dealate queen from Sabah is tentatively identified with this species. TL 6.9, HW 1.22, HL 1.25 (CI 98), ML 1.69 (MI 136), SL 1.48 (SI 121), EL 0.77, HFL 1.59 (TWI 20), WL 1.93 mm. Granulate sculpture similar but relatively stronger than holotype, as in other material from Borneo (see below). Trunk granulate dorsally, much more feebly granulate on sides; propodeum conspicuously sculptured, transversely granulo-rugose dorsally, obliquely so on sides, with declivity virtually smooth. Uniform rich dark orange red, mandibles, antennae and legs slightly lighter.

Additional Records. BORNEO: *Sarawak*: Fourth Div., Gunung Mulu Nat. Park, RGS Exped., Long Pala, leaf litter, lowland rainforest, 6.X.1977, six workers (B. Bolton, BMNH and MCZ). *Sabah*: Bukit Sulong nr. Lamunin, 4.IX.1982, one dealate queen (N. Stork, BMNH). PENINSULAR MALAYA: Malaysia, Selangor, Ulu Gombak Forest Reserve, 24.VIII.1967, tree lookout area, ca. 450 m, hill forest, one worker (R. Crozier, MCZ); Singapore, Bukit Timah Nat. Reserve, 1 Nov. 1982, in leaf litter on forest floor, one worker (D. H. Murphy and M. W. Moffett, MCZ).

Workers from these regions are similar to the Javanese holotype (including palpal segmentation of 5,3 in all workers examined), but, with the exception of the queen described above, are significantly smaller (HW for workers 1.01 to 1.07 mm; TL 5.8 to 6.1 mm, except Singapore specimen 5.5

mm) and with slightly narrower heads (CI 92 to 96 for all workers); fine rugae on metanotum transverse (continuing partially down sides in Singapore specimen); metanotal groove conspicuously impressed; and with petiole node similar to that described for *M. binghami*: less massive and with a steeper posterior face than in holotype. The Singapore specimen has an exceptionally narrow petiole node. Specimens from Borneo (including the queen described above) are slightly darker in color, have a more strongly developed iridescence and a somewhat stronger granulate sculpturing (but still not as strong as in *M. ceylonicum*); the sculpture continues on occiput (and even feebly beneath head on Sabah queen described above) and on to sides of pronotum and propodeum.

Synonymy. On the basis of Wheeler's (1933) description, the holotype worker of *M. kemneri* is apparently very similar to the *barbouri* type, but is smaller (length given as 6.0 mm, versus 6.9 mm given by Wheeler for the *barbouri* holotype) with a more conspicuous granulate sculpture, slightly darker coloration, and with the petiole having a "distinctly thicker and apically more rounded node" (Wheeler, 1933). These differences are similar to those between the *barbouri* holotype and the Borneo specimens described above.

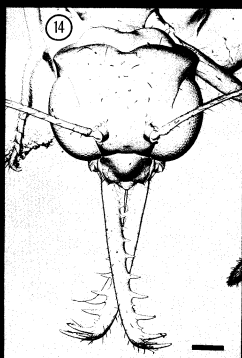
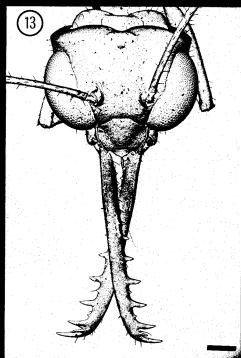
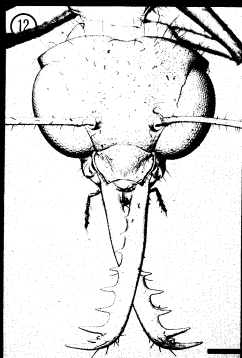
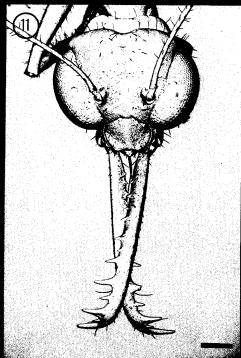
Natural History. A worker collected in leaf litter at Bukit Timah National Park in Singapore (Fig. 2) could not be induced to capture prey. However, its distinctive movement patterns were so similar to those observed for foragers of *M. toro* from Sulawesi that there can be little doubt *M. barbouri* is also predacious.

Figures 11–14. The *binghami* group. Frontal views of the worker head. 11. *M. barbouri* from Sarawak. 12. *M. binghami* from Thailand. 13. *M. inodum* paratype. 14. *M. mjoebergi* syntype.

Scale lines. 0.25 mm.

Figures 15–18. The *binghami* group. Lateral views of the worker trunk and gaster. 15. *M. barbouri* from Sarawak. 16. *M. binghami* from Thailand. 17. *M. inodum* paratype. 18. *M. mjoebergi* syntype (uncoated).

Scale lines. 0.25 mm.





Myrmoteras binghami

Figures 12, 16; Map 1

Myrmoteras binghami Forel, 1893: 607. Thaungyin Valley (Tenasserim), Burma, May 1893, 2 worker syntypes (Bingham, Forel Coll. [examined]). Worker redescribed by the following: Forel, 1894: 419; Bingham, 1903: 314, fig. 95; Emery, 1925: pl. 1, fig. 10, pl. 2, fig. 1; Creighton, 1930: 186, fig. 2, pl. 11, fig. 2.

Diagnosis. With short decumbent pilosity and minute punctures on the dorsum of the head and pronotum.

Worker. Syntypes (two measured): TL 5.9 mm, HW 1.15 to 1.16, HL 1.15 to 1.17 (CI 99 to 100), ML 1.41 to 1.43 (MI 122), SL 1.38 to 1.40 (SI 120 to 121), EL 0.75, HFL 1.47 to 1.51 (TWI 18 to 20), WL 1.65 to 1.68 mm. Frontal sulcus a very feeble impressed line (Fig. 12)—not conspicuous as has been stated by authors from Creighton (1930) on. Palpal segmentation 6.4 (one worker checked). Frontal area present but poorly demarcated. Mandibles with 8 to 9 teeth and no preapical denticles; two apical denticles.

Pronotum and propodeum slightly flattened above, dorsal face of propodeum shifting to declivity relatively abruptly so as to form a weakly apparent angle (more rounded in other species). Metanotal groove conspicuously impressed. Node of petiole with anterior face precipitous and virtually straight, posterior face not as steep; summit slightly flattened. Ventral margin of petiole feebly concave beneath node.

Pronotum and dorsal surface of head smooth except for numerous minute punctures 0.01 to 0.02 mm apart, including on clypeus; on gaster punctures more widely scattered and weaker; elsewhere with punctures virtually absent. Mesothorax with two to four ill-defined longitudinal rugae low on sides, smooth or with very weak longitudinal wrinkles dorsad; propodeum smooth, although surface very slightly irregular dorsad. In addition to the long, erect to suberect hairs found in other *Myrmoteras* species, with numerous very short, fine decumbent to subdecumbent

hairs dorsad on head, pronotum and propodeum and present but less dense and conspicuous on the legs and gaster (one of the syntypes virtually lacks any pilosity dorsad on the head but is otherwise similar to the other; presumably the hairs have been worn off of this area). The long, prominent hairs moderately dense, with 11 to 19 hairs breaking dorsal margin of trunk viewed in profile. Hairs short, rising to 0.08 mm on head and 0.12 mm on trunk and gaster. Two or three hairs on or near each metathoracic tubercle; node of petiole with five to seven hairs. Bright reddish orange, with gaster yellowish brown; petiole, legs, and mandibles orange yellow; and antennae yellowish orange.

Additional Records. BURMA: Thaungyin Valley, one worker (Emery Coll.). THAILAND: Mae Sa [presumably Mae Sai], 19.VII.1975, three workers (D. Jackson, BMNH and MCZ). Burmese specimens similar to syntypes and may be part of the same series. Thailand specimens very similar to syntypes (HW 1.14 to 1.18; TL 5.7 to 5.9 mm; palpal segmentation consistently 6.4) but with relatively shorter mandibles and scapes (MI 128 to 131; SI 112 to 114); much more prominent, smoothly-rounded longitudinal rugae both dorsally and laterally on mesothorax; mesothorax orange, lighter than remainder of trunk; hairs on trunk longer (0.15 mm) and more numerous (29 to 41 breaking dorsal margin in profile); node of petiole with 9 to 11 hairs.

Myrmoteras iriodum new species

Figures 13, 17; Map 1

Holotype. Worker deposited in MCZ from Borneo: SE Kalimantan: 17 to 46 km W. Batulitjin, 28 June to 2 July 1972, lowl. rainfor., hollow stick in litter, B-18, (W. L. Brown). Name a noun in apposition from *Gr. iroides*, referring to the relatively strong iridescence on the head and trunk.

Diagnosis. Head smooth, lacking sculpture. Distinguished from *M. mjoebergi* by its relatively long mandibles (ML > 1.30), relatively strong iridescence, five-seg-

mented maxillary palps, and by the dense pilosity.

Worker. Holotype (HW 1.20) and five paratypes: TL 6.4 to 6.8, HW 1.14 to 1.20, HL 1.17 to 1.22 (CI 97 to 99), ML 1.68 to 1.74 (MI 142 to 145), SL 1.36 to 1.40 (SI 115 to 120), EL 0.72 to 0.76, HFL 1.49 to 1.56 (TWI 17 to 19), WL 1.80 to 1.85 mm. Only a trace of the frontal sulcus is visible. Trigger hairs unusually short, projecting only ca. 0.45 to 0.50% of distance to mandible tips (ca. 75 to 90% in randomly selected individuals from other species except for two [of four measured] *M. binghami* specimens with measurements of ca. 60%). Palpal segmentation 5,3 (three specimens examined). Mandibles relatively longer than in other species of the subgenus, and with 11 to 13 teeth (usually 12) and 2 to 3 preapical denticles (usually two); apical denticle pair with distal denticle unusually massive, stout. Distal portion of mandible shafts somewhat less strongly bent downward than in *M. mjoebergi*.

Pronotum low and evenly convex; propodeum slightly flattened above. Metanotal groove conspicuously impressed. Node of petiole distinctive, similar to *M. mjoebergi*, but taller and more massive, with anterior face a long vertical drop; summit narrow (relative to base) and rounded; posterior face sloping, slightly convex to straight. Summit of node evenly rounded when viewed from behind. Ventral margin of petiole feebly convex to virtually straight beneath node.

Head and trunk only very feebly lustrous, but more strongly iridescent than in other species, and with other parts of the body more feebly iridescent. Head, pronotum and propodeum smooth (very slight surface irregularities could possibly represent traces of a granulate sculpture); mesothorax very feebly and irregularly rugose dorsad, where rugae are largely transverse. Laterally mesothorax irregularly sculptured with narrow rugae, and in some cases with a narrow ruga extending forward to pronotum from base of

metathoracic tubercle, much as in most species of the *donisthorpei* and *bakeri* groups of *Myagroteras*. Pilosity dense to very dense, with 33 to 42 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.08 mm on head and 0.10 mm on trunk and gaster. Two or three hairs on or near each metathoracic tubercle; node of petiole with 8 to 14 hairs. Orange with slight reddish tinge, virtually uniform except trunk slightly darker reddish orange and gaster orange yellow.

Queen. Paratype: TL 7.0, HW 1.23, HL 1.24 (CI 101), ML 1.68 (MT 135), SL 1.38 (SI 110), EL 0.77, HFL 1.54 (TWI 18), WL 1.90 mm. Trunk smooth, although possibly with traces of a granulate sculpture; propodeum feebly and irregularly transversely rugose dorsad. Head very feebly longitudinally rugose between bases of antennae.

Paratypes. Six workers with same date and collection number, and one dealate queen with same data but labelled "abandoned earthen termite nest" (MCZ, BMNH).

Additional Records. BORNEO: *Sarawak:* Fourth Div., G. Mulu Nat. Park, RGS Exped., Long Pala, lowl. rainfor. in leaf litter, 13.X.1977, two workers (B. Bolton, BMNH and MCZ). *PENINSULAR MALAYA:* Selangor, Gombak, 9.X.1973, one worker (B. Bolton, BMNH). All these specimens are similar in size and proportions to the type series (Sarawak workers HW 1.20, 1.28 mm; TL 6.6, 7.0 mm; Gombak worker HW 1.17 mm; TL 6.4 mm), but are somewhat darker (head and trunk orange red to reddish orange, appendages lighter); and with propodeum having very fine, weak, mostly transverse rugae dorsad and behind. Gombak specimen with shape of petiole very similar but with node not as wide and massive as in type series.

Myrmoteras mjoebergi

Figures 5, 14, 18; Map 1

Myrmoteras mjoebergi Wheeler, in Creighton, 1930: 188, fig. 2, pl. 11, fig. 1. Borneo: Mt. Tobangs (top)

(Bukit Tabong? [Sarawak]) 1,700 m, 3 worker paratypes. (E. Mjöberg, MCZ [examined]).

Diagnosis. Head smooth, lacking sculpture. Distinguished from *M. iriodum* by its shorter mandibles ($MI < 130$), four-segmented maxillary palps, low, rounded petiolar node, and greatly reduced pilosity.

Worker. Syntypes (three measured): TL 5.6 to 6.0, HW 1.02 to 1.08, HL 1.12 to 1.18 (CI 91 to 92), ML 1.26 to 1.31 (MI 111 to 112), SL 1.21 to 1.27 (SI 116 to 119), EL 0.66 to 0.71, HFL 1.43 to 1.55 (TWI 17 to 18), WL 1.60 to 1.70 mm. Frontal sulcus absent (slightest trace between antennae in some lights). Palpal segmentation consistently 4.3. Mandibles with 10 to 12 teeth (usually 10) and one to two preapical denticles (usually two); apical pair with larger (most distal) denticle thinner and generally coming to a sharper point than in other species in the *binghami* group.

Pronotum higher and more rounded than in other species in the subgenus; propodeum also convex, slightly flattened dorsad in one specimen. Metanotal groove not visible as a conspicuously impressed notch in profile. Propodeum evenly and feebly convex in profile. Node of petiole low, rounded; anterior face more precipitous. Ventral margin of petiole feebly convex or feebly concave beneath node.

Head and trunk smooth, lacking punctures or other traces of sculpture outside of poorly defined longitudinal rugae on sides of mesothorax. Hairs short and sparse, rising about 0.10 mm, with 8 to 12 rising above dorsal margin of trunk in profile. Metathoracic tubercle hairs one or none; node of petiole with ca. five to seven hairs. Head and trunk uniform orange red, petiole orange, gaster yellow brown; legs, antennae, and mandibles strongly contrasting orange yellow.

Additional Records. Known only from type series.

THE CEYLONICUM GROUP

Small to medium species (worker 3.9 to 5.5 mm TL). Head broad (CI > 108); oc-

cipital lobe slightly less massive than in *binghami* group (OLI 5 to 8). Orbital grooves moderately developed, more conspicuous than in the *binghami* species group. Frontal area present but poorly demarcated (absent in *brachygnathum*). Ridges above antennal bases moderately developed. Palpal segmentation variable; known extremes 6.4 and 3.3 (4.2 in *M. scabrum*?). Mandibles conspicuously shorter than in any other species, no longer than head (MI less than 102). Number of mandibular teeth eight to nine; apical denticles both present, but small. Head and trunk lustrous, completely lacking the feeble iridescent sheen typical of the *binghami* group.

This distinctive group includes three species from southern India and Sri Lanka, all of which have been collected in areas of evergreen forest at moderate to high elevations (600 to 2,200 m).

Myrmoteras brachygnathum new species Figures 19, 22; Map 1

Holotype. Worker deposited in MHN from India: Tamil Nadu: Palni Hills, south of Kodaikanal, 2,200 m, 12.XI.72, #23 [tamisages dans forêt dégradée avec rhododendrons] (Besuchet and Löbl). Name derived from *Gr. brachys* + *gnathum*, referring to the relatively short mandibles of the females.

Diagnosis. Easily distinguished from *M. ceylonicum* and *scabrum* by the lack of sculpture on the head and pronotum.

Worker. Holotype: TL 3.9, HW 0.92, HL 0.85 (CI 109), ML 0.73 (MI 86), SL 0.90 (SI 97), EL 0.56, HFL 0.94 (TWI 20), WL 1.18 mm; paratype worker from same series TL 4.0, HW 0.93 mm, and otherwise virtually identical to holotype. Only a trace of the frontal sulcus is visible. Frontal area not demarcated. Clypeus highly convex, with curvature continuing to lateral margins, as in *M. ceylonicum* but unlike any other species in the subgenus. In *M. brachygnathum* the clypeus also exceptionally narrow, only 23 to 25% wider than long (greater than 35% for single specimens selected at random from all other species in the genus, including *cey-*

lonicum). Palpal segmentation of type 3,3 (in paratype worker 4,3). Mandibles with one to two preapical denticles. Curvature of distal ends of mandible shafts ventrad stronger than described for *M. ceylonicum* but still relatively weak; bend at penultimate tooth about 30 to 40°.

Pronotum low and evenly convex or slightly flattened; propodeum rounded, summit somewhat higher than mesothorax (virtually level with mesothorax in other species in the subgenus). Metanotal groove conspicuously impressed. Node of petiole tall, with nearly vertical posterior face and very steep, straight anterior face; summit slightly flattened, but lacking the transverse ridges found in *M. ceylonicum* and *scabrum*. Spurs on middle and hind tibiae shorter than in other members of the subgenus, longest with a length of about twice the width of the base of the first tarsal segment.

Head, pronotum and propodeum smooth and polished, lacking sculpture. Mesothorax with two to three narrow longitudinal rugae on sides, weaker longitudinal rugae dorsally. Pilosity considerably reduced in comparison to *M. ceylonicum* and *scabrum*, with hairs sparse, 2 to 10 breaking dorsal margin of trunk in profile. Hairs rising 0.08 to 0.10 mm on head, trunk, and gaster. One or no hairs on or near each metathoracic tubercle; node of petiole with two to four hairs. Head and trunk translucent yellowish orange (rugae on mesothorax darker), antennae same but lighter; petiole orange yellow, legs and mandibles lighter orange yellow; gaster very dark orange brown.

Queen. Dealates from type series (one measured; other virtually identical), TL 4.3, HW 1.03, HL 0.92 (CI 112), ML 0.81 (MI 88), SL 0.98 (SI 95), EL 0.63, HFL 1.03 (TWI 20), WL 1.33 mm; very similar in shape and proportions to worker except for more massive trunk; petiole similar but narrower at summit. Trunk entirely smooth and shining, reddish orange; otherwise color same as in workers.

Paratypes. One worker and two dealate queens with same locality data and col-

lection number as holotype (MCZ and MHN).

Additional Records. INDIA: Tamil Nadu: Kodaikanal, 17.4.27, one dealate queen (C. Escher, MHN); Palni Hills, 7 km east of Kodaikanal, 1,750 m, 12.XI.1972, #24 [tamisages en forêt], 23 workers (Besuchet and Löbl, MHN, MCZ, MCSN); Palni Hills, 10 km east of Kodaikanal, 2,150 m, 15.XI.1972, #27 [tamisages en lisière de forêt, avec rhododendrons et fougères, près d'une rivière], one worker, three dealate queens (Besuchet and Löbl, MHN); Anaimalai Hills, 18 km north of Valparai, 1,250 m, 18.XI.1972, #35 [tamisages en forêt], four workers, one dealate queen (Besuchet, Löbl, and Mussard, MHN, BMNH, MCZ). Palpal segmentation 4,3 in all females checked (at least four in each series, when available); pilosity consistently sparse, with no more than 15 hairs breaking dorsal margin of trunk in profile.

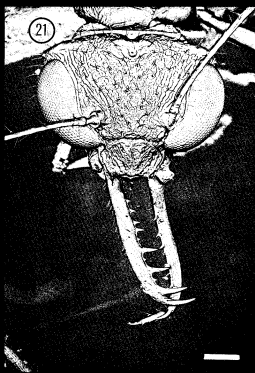
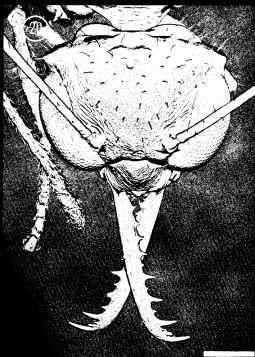
Myrmoteras ceylonicum

Figures 20, 23; Map 1

Myrmoteras ceylonica Gregg, 1956: 41, fig. 1. Sri Lanka: Udawaddakele Sanctuary, Kandy, 2,000 ft, VII.13.1955, #1243, three workers (E. O. Wilson, holotype in MCZ [examined]; paratypes in collection of R. E. Gregg). Name changed to correspond in gender with genus.

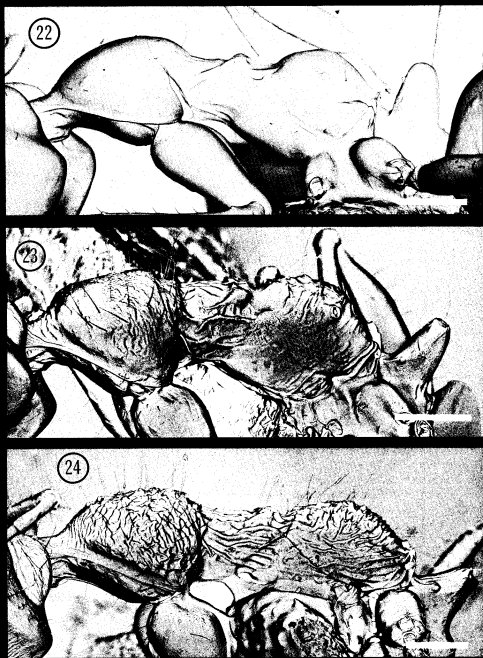
Diagnosis. Head and trunk conspicuously sculptured. Distinguished from *M. scabrum* by its smaller size; evenly granulate head sculpture; relatively feeble mandibular bend; dorsally flattened pronotum; node of petiole taller than wide in side view; and lighter color.

Worker. Holotype: Length excluding missing gaster 3.1 mm (est. original TL 4.0 mm), HW 0.94, HL 0.83 mm (not 0.90 mm, as Gregg [1956] reported) (CI 113), ML 0.83 (MI 100), SL 0.85 (SI 90), EL 0.56, HFL 0.95 (TWI 28), WL 1.17 mm. Size small. Frontal sulcus very feeble, a narrow smooth line extending from just above clypeus to median ocellus. Frontal area poorly defined. Clypeus strongly convex, as described for *M. brachygnathum*



Figures 19–21. The *ceylonicum* group. Frontal views of the worker head. 19. *M. brachygnathum* paratype. 20. *M. ceylonicum* holotype (uncoated; oil slightly obscures sculpture). 21. *M. scabrum* holotype (uncoated).

Scale lines, 0.25 mm.



Figures 22–24. The ceylonicum group. Lateral views of the worker trunk and gaster. 22. *M. brachygnathum* paratype. 23. *M. ceylonicum* holotype (uncoated; oil slightly obscures sculpture). 24. *M. scabrum* holotype (uncoated).

Scale lines. 0.25 mm.

but not as narrow. Scapes relatively short, overreaching posterior border at 62% of their length. Palpal segmentation 6.4. Mandibles with 3 to 4 preapical denticles. Mandible shafts weakly bent downward distally, so that when seen from above with the proximal portions of the shafts in the plane of view both the apical tooth and apical denticles are clearly visible; bend at penultimate tooth only about 35°.

Pronotum and propodeum flattened dorsad. Metanotal groove conspicuously impressed. Petiole with node narrow, much taller than broad in side view, with steep, virtually straight sides and a flat or slightly concave summit with feeble ridges along the apices of the anterior and posterior faces; short and squat when viewed from behind. In holotype curvature of ventral margin of petiole beneath node uncertain because of obscuring glue (illustration of Gregg [1956], which is of doubtful value because it is based on the same specimen, shows ventral margin virtually straight except for a small scooped-out area near the anterior peduncle). Tibia of the single intact middle leg on the holotype strongly dilated (in other species in the subgenus TWI 16 to 22).

Dorsal surface of head evenly granulate, with grains ca. 0.01 to 0.02 mm in diameter; clypeus finely granulo-rugose; back of head smooth. Smooth laterally beneath eyes except for faint longitudinal rugae; ventrum of head smooth. Pronotum more weakly granulate than head, smoother laterally; mesothorax with 2 to 3 widely spaced longitudinal rugae on sides and more numerous and weaker longitudinal rugae above; propodeum almost smooth laterally, dorsally and behind with narrow, relatively straight and evenly spaced transverse rugae ca. 0.03 mm apart. Pilosity long and dense, with 37 hairs breaking dorsal margin of trunk viewed in profile. Hairs rising 0.13 mm on head and 0.20 mm on trunk. Two prominent hairs on or near each metathoracic tubercle; six hairs on node of petiole. Reddish orange but with petiole, legs, gaster and

antennae orange yellow and mandibles lighter orange yellow.

Additional Records. Known only from type series.

Myrmoterus scabrum new species

Figures 21, 24; Map 1

Holotype. Worker deposited in MCZ from India: Kerala State: Cannanore Dist.: Peria Reserve (Western Ghats), 4-5.IV.1969, ca. 900 m, evgrn. for. (A. B. Soans and W. L. Brown). Name derived from Latin *scabra*, referring to the heavily sculptured head and trunk.

Diagnosis. Head and trunk conspicuously sculptured. *M. scabrum* can be distinguished from closely related *ceylonicum* by its larger size; the stronger granulo-rugose sculpture on the head; very conspicuous mandible bend; evenly convex (rather than flattened) pronotum; node of petiole wider than tall in side view; and much darker color.

Worker. Holotype: TL 5.5, HW 1.25, HL 1.12 (CI 112), ML 1.13 (MI 101), SL 1.31 (SI 105), EL 0.73, HFL 1.38 (TWI 16), WL 1.68 mm. Larger than *M. ceylonicum* and *brachygnathum*. Frontal sulcus absent, although a weak medial ridge extends from clypeus to a point just above antennal bases. Frontal area present, better defined than in *M. ceylonicum*. Scapes relatively longer than in *M. ceylonicum* holotype, overreaching posterior border of head at about 50% of their length. Clypeus raised medially somewhat more prominently than in most species in the subgenus but not to the degree found in *M. ceylonicum* and *brachygnathum*; clypeal teeth exceptionally strong. Maxillary palps four, labial palps apparently two. Mandibles with two to three preapical denticles; shafts strongly bent at tips, so that when seen from above with the proximal portions of the shafts in the plane of view the apical tooth and apical denticles are virtually directly behind the penultimate tooth. Mandibles relatively strongly depressed, 46% wider than deep

at position of fifth tooth (about half way to apex); in single specimens selected at random from each of the other species in the subgenus the mandibles varied from 26 to 35% wider than deep at this point.

Trunk as described for *M. ceylonicum* but propodeum less strongly depressed. Anterior and (except at base) posterior faces of petiolar node virtually straight, with the anterior face steeper, meeting peduncle rather abruptly at an obtuse angle; posterior face curving gently into posterior peduncle. Summit of node flat or slightly concave in profile as in *M. ceylonicum*, with ridges along anterior and posterior apices somewhat better developed. Node 20% broader than high, versus 45% higher than broad in *ceylonicum*. Middle and hind tibiae only slightly swollen, parallel sided throughout most of their lengths.

Dorsal surface of head densely granulorugose, coarser (grain ca. 0.02 to 0.03 mm across) and more irregular than in *M. ceylonicum*; this sculpturing weaker and less dense on clypeus (which is virtually smooth mesad) and on back of head. Smooth laterally beneath eyes except for faint longitudinal rugae; ventrum of head smooth. Pronotum densely and very irregularly rugose, rugae largely transverse; mesothorax with prominent longitudinal rugae ca. 0.04 mm apart dorsad and laterally; similar rugae laterally on propodeum. Propodeum dorsally and behind with narrow transverse rugae as in *M. ceylonicum* but more closely spaced, ca. 0.02 to 0.03 mm apart. Gaster and legs smooth and shining. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk in profile. Hairs long, rising to 0.15 mm on head and 0.20 mm on trunk and gaster. Two hairs on or near each metathoracic tubercle; node of petiole with two rows of five to six well-spaced hairs along anterior and posterior ridges and down onto sides of node. Very dark orange red with legs and gaster relatively lighter and antennae and mandibles yellowish orange; tarsi yellow.

Additional Records. Known only from holotype.

Subgenus *Myagroteras* new subgenus

Type. *Myrmoteras donisthorpei* Wheeler, by present selection. Name derived from Gr. *myagra* + *teras*, in reference to the trap-jaw prey capture technique.

Females lacking the long trigger hairs characteristic of the subgenus *Myrmoteras*; instead labrum with a pair of short but conspicuous hairs (length less than 10% of mandible length). Dorsal surface of labrum (that is, the surface visible in dorsal full face view) not coming to a distinct anterior point; instead anterior margin rounded or truncate. The paired hairs originate well apart somewhat below the dorsal labral surface, and thus they are apparently positioned relatively lower on labrum than are trigger hairs in the subgenus *Myrmoteras*. The hairs are straight, and extend forward and strongly ventrad. Although more slender and differing somewhat in position, these hairs are possibly homologous with the trigger hairs found in the subgenus *Myrmoteras*.

In contrast to the subgenus *Myrmoteras*, frontal sulcus strongly developed, a conspicuous narrow to moderately wide groove (maximum width at least 0.01 mm) extending from the frontal area to the median ocellus (the single exception is *M. insulcatum*, which completely lacks the sulcus). Both the orbital grooves and the ridges above antennal bases present, moderately developed to conspicuous. Frontal area demarcated to some degree. Except for the species *M. insulcatum*, clypeus higher and more strongly convex medially than in the subgenus *Myrmoteras*, and with lateral flanges better defined because of a more sudden shift in plane relative to the margins of the median region.

Mandibles relatively longer than in *Myrmoteras*, usually as long as or longer than trunk ($ML/WL > 0.95$ except in some *M. morowali* and *indicum* workers). Mandible shafts very feebly bent ventrad

at position of penultimate tooth, angle of bend 20° or less (Fig. 6B); bend strongest in *M. williamsi*. When viewed from above outer margins of shafts feebly convex as in *Myrmoteras*, but often with a subtle inward bend at about a third of the distance from the mandible bases to the apical tooth (Fig. 27; essentially lacking in *M. toro*, *diastematum*, and some *donisthorpei* workers). Apical denticles relatively poorly developed, often smaller than in the subgenus *Myrmoteras*, with the largest invariably less than 18% of the length of the apical tooth.

Myagroteras species tend to be small, with none having head widths exceeding 1.10 mm. None of these ants has the feeble iridescence on the head and trunk characteristic of the *Myrmoteras* species in the *binghami* group.

This subgenus contains 11 species distributed from India to the Philippines. To date the greatest number of *Myagroteras* collections have been made in Borneo. The worker caste is known for ten species; the queen for nine; and males for four.

Two males have been collected from Hainan Island; one from Tien Fong Mountains is in the British Museum (Natural History) and the other (from Ta Han) is in the Museum of Comparative Zoology. Both are very similar to males of *M. bakeri* and *donisthorpei* and are therefore presumably in the subgenus *Myagroteras* (no males from the subgenus *Myrmoteras* have been described).

THE BAKERI GROUP

Mostly medium-sized (female size range 4.2 to 6.0 mm); smallest species *M. bakeri*. Palpal segmentation varying from 5.3 to 4.2. Head and pronotum smooth, lacking sculpture, or with only traces of rugae. Rugae above antennal bases often conspicuous. Mandibles often with only a single apical denticle. Narrow ruga extends forward from base of each metathoracic tubercle as in the *donisthorpei* group (but absent in *M. bakeri*). Metanotal groove not

visible as a conspicuously impressed notch in profile (but notch feebly developed in some *M. bakeri*). Ventral margin of petiole feebly convex beneath node.

Two species in this group are from Malaysia (including Sarawak and Sabah) and the third is from southern India.

Myrmoteras bakeri

Figures 25, 28; Map 2

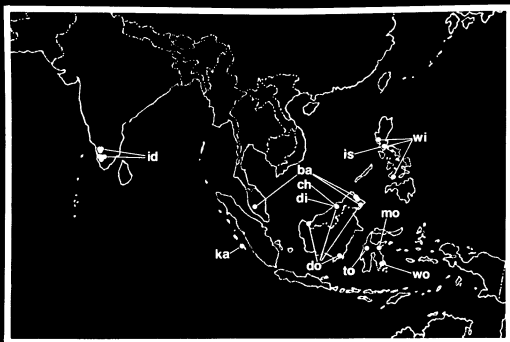
Myrmoteras bakeri Wheeler, 1919: 145. Borneo: Sabah: Sandakan, 1 queen and 3 males (Baker, MCZ [examined]). Creighton, 1930: 184, pl. 11, fig. 5.

Diagnosis. Females can be distinguished from other species in the *bakeri* group by the absence of a wide sulcus between the clypeus and frons; the lack of a prominent ruga extending forward from each metathoracic tubercle; the presence of two apical denticles on each mandible; and the relatively dilated tibiae (TWI > 23).

Workers. Described for the first time. The following description applies to two workers from Sabah collected by Leakey. TL 4.6, HW 0.86 to 0.89, HL 0.88 (CI 98 to 102), ML 1.33 to 1.34 (MI 152 to 153), SL 0.94 to 0.95 (SI 107 to 109), EL 0.56 to 0.58, HFL 0.94 to 0.96 (TWI 26 to 27), WL 1.23 to 1.25 mm. Frontal sulcus a narrow, very shallow trench; orbital grooves conspicuous. Frontal area clearly defined. Palpal segmentation 5.3 (both inspected). Mandibles with 11 to 12 teeth and two preapical denticles. With two very tiny and sharp apical denticles, the smallest minute.

Pronotum low and evenly convex; propodeum feebly convex, and with summit virtually level with mesothorax; metanotal groove visible as a feebly impressed notch in profile. Node of petiole in profile with nearly vertical anterior face. Tibiae strongly dilated as in *M. donisthorpei*, but unlike other members of the *bakeri* and *williamsi* groups, which have feebly dilated tibiae.

Head smooth except for traces of very fine longitudinal rugae between antennal



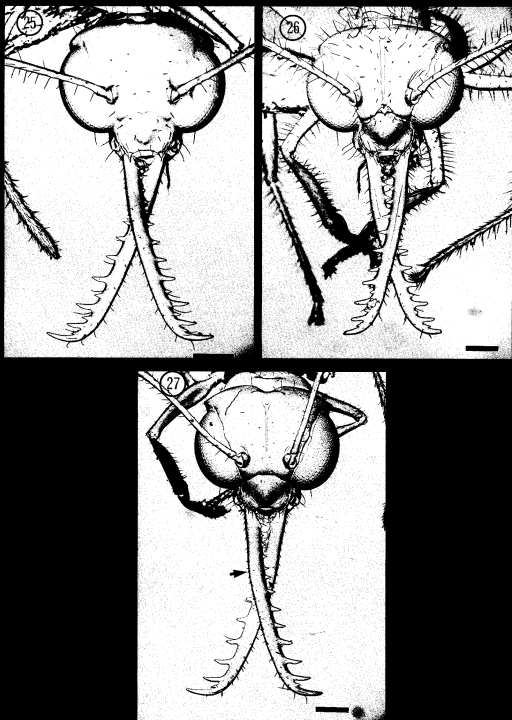
Map 2. Distribution of species in the subgenus *Myrmoteras*.

Abbreviations: ba = *M. bakeri*, ch = *M. chondrogastrium*, di = *M. diastematum*, do = *M. donisthorpei*, id = *M. indicum*, is = *M. insulcatum*, ka = *M. karnyi*, mo = *M. morowali*, to = *M. toro*, wi = *M. williamsi*, wo = *M. wolasi*.

bases and rugae curving above antennal fossae. Pronotum smooth but with traces of longitudinal rugae dorsally; dorsum of mesothorax feebly granulate with delicate transverse rugae, laterally smooth except for feeble oblique or longitudinal rugae; propodeum with very fine transverse rugae dorsally, extending obliquely over sides, posterior declivity smooth. Pilosity moderately dense, with 19 to 21 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.06 mm on head and 0.10 mm on trunk and gaster; two to three hairs on or near each metathoracic tubercle; five to six on node of petiole. Uniform yellowish orange with appendages and petiole lighter, orange yellow (femora and coxae virtually white); gaster darker. Head translucent as in queen.

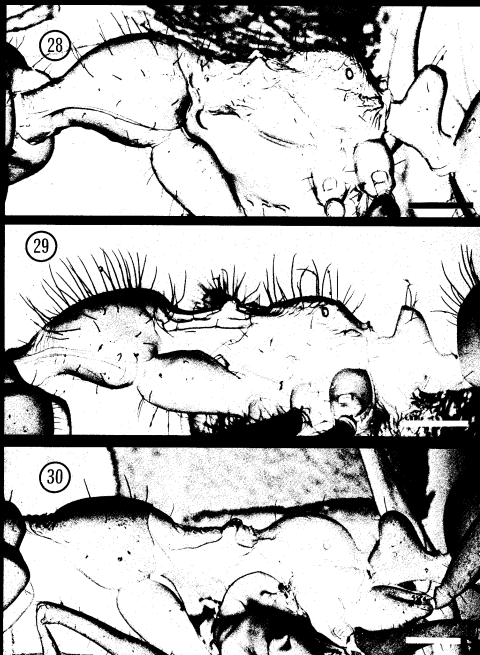
Queen. Holotype with head, petiole and gaster lost: HFL 0.87 (TWI 24), WL 1.18

mm. A second queen from the same region, apparently very similar to holotype: TL 4.2, HW 0.82, HL 0.83 (CI 100), ML 1.23 (MI 148), SL 0.88 (SI 106), EL 0.54, HFL 0.85 (TWI 26), WL 1.15 mm. Creighton (1930) states that the mandibles of the holotype had nine teeth and two preapical denticles, as well as only a single apical denticle; the other queen has 10 to 11 teeth and two preapical denticles, as well as a pair of tiny apical denticles, as in the workers. Trunk smooth except for very feebly rugulose sculpture on mesonotum near scutellum; propodeum transversely rugose dorsad, these rugae extending obliquely onto sides; rugae ca. 0.01 mm across. Trunk of holotype yellowish orange, lighter than in workers, with petiole and legs pale yellow, femora, trochanters and coxae virtually white; the other queen is similarly colored, with the



Figures 25–27. The *bakeri* group. Frontal views of the worker head, 25. *M. bakeri* from Sabah (fine layer of oil obscures frontal sulcus), 26. *M. diasternatum*, 27. *M. indicum* paratype (arrow indicates location of mandibular angle).

Scale lines. 0.25 mm.



Figures 28–30. The *bakeri* group. Lateral views of the worker trunk and gaster. 28. *M. bakeri* from Sabah. 29. *M. diasternatum*. 30. *M. indicum* paratype.

Scale lines. 0.25 mm.

head concolorous with trunk and translucent, as had been described for the holotype (Creighton, 1930). This translucence is of doubtful taxonomic value, because the head is opaque in a Malayan *M. bakeri* specimen. Some specimens of *M. diastematum* and *M. indicum* also have relatively translucent integuments.

Male. Paratypes (two measured): HW 0.63, HL 0.68 (CI 93), SL 0.78 to 0.83 (SI 124 to 132), EL 0.35 to 0.37, WL 1.04 to 1.09 mm. Frontal sulcus a feebly impressed medial line. Palpal segmentation 5.3. Head smooth; mesonotum and scutellum longitudinally rugulose, rugae ca. 0.01 to 0.02 mm across; pronotum and anepisternum much more feebly rugulose; kat-episternum and propodeum with conspicuous raised rugae; these extend mostly longitudinally on sides and transversely dorsad and on posterior declivity. Sculpture on trunk interspersed with a little granulate sculpture.

Additional Records. BORNEO: *Sabah:* Gunung Silam, 620 m, 1983, A15-3.1, two workers (R. Leakey, BMNH and MCZ); Bettotan near Sandakan, 12 Aug. 1927, one alate queen (C. B. K. and H. M. P., BMNH). PENINSULAR MALAYA: Selangor, Gombak, 9.X.1973, one worker (B. Bolton, BMNH). Worker from the Malay Peninsula slightly smaller in size than the Sabah workers (TL 4.2, HW 0.83), but very similar in proportions; rugae between antennal bases more prominent but still feeble; propodeum much more feebly rugulose, with dorsum essentially smooth; metanotal groove poorly defined; with a feeble groove running most of the length of each mandible dorsally, as in *M. diastematum* and *morowali* females.

Myrmoteras diastematum new species
Figures 26, 29; Map 2

Holotype. Worker deposited in BMNH from Borneo: Sarawak: 4th Division: Gunung Mulu National Park, v-viii.1978, B. M. 1978-49, camp 2 (P. M. Hammond and J. E. Marshall). Name derived from *Gr. diastema*, referring to the wide sulci on the head.

Diagnosis. The conspicuous sulcus between the clypeus and frons is unique to this species; this and the exceptionally wide frontal sulcus and orbital grooves serve to readily distinguish the species from closely related *M. bakeri*.

Worker. Holotype: TL 5.4, HW 0.98, HL 1.03 (CI 95), ML 1.53 (MI 149), SL 1.19 (SI 122), EL 0.64, HFL 1.28 (TWI 18), WL 1.50 mm; two other workers HW 1.01 and 1.10 mm. Frontal sulcus, orbital grooves, and gap between clypeus and head capsule wide, forming conspicuous trenches bordered in black. Frontal area clearly defined. Palpal segmentation 5.4 (three inspected). Mandibles with 8 to 11 teeth and 3 to 4 preapical denticles. Either one or two apical denticles, the smallest, when present, being very minute, and the largest somewhat more massive than that of *M. bakeri*. Mandibular groove present, extending medially down shafts as described for *M. morowali*.

Shape of trunk and petiole as in *M. bakeri*, but petiolar node not as high and posterior face less steep.

Head smooth except for rugae curving above antennal bases; pronotum smooth except for a few short longitudinal rugae on anterior face extending up from neck; mesothorax with several well separated narrow longitudinal rugae laterally, and feebly granulate dorsally, with indistinct fine longitudinal rugae. Propodeum dorsally with feeble narrow transverse rugae ca. 0.01 to 0.02 mm apart which fade out on sides at about level of spiracle; declivity virtually smooth. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk when viewed in profile. Hairs long, rising 0.13 to 0.15 mm on head and 0.18 to 0.20 mm on trunk and gaster; 3 to 4 hairs on or near each metathoracic tubercle and 8 to 11 on node of petiole. Lighter in color than other *diastematum* material, including paratype queen described below, and thus probably somewhat teneral: head orange; legs darker orange; trunk and petiole yellowish orange;

antennae and mandibles orange yellow; gaster brownish red.

Queen. Paratype with same collection number as holotype (HW 0.98) and two other Sarawak queens measured: TL 5.4 to 6.0, HW 0.98 to 1.06, HL 1.01 to 1.10 (CI 94 to 97), ML 1.43 to 1.56 (MI 141 to 142), SL 1.14 to 1.28 (SI 117 to 123), EL 0.63 to 0.68, HFL 1.23 to 1.35 (TWI 17 to 19), WL 1.50 to 1.68 mm. Mesonotum with conspicuous longitudinal rugae dorsally; remainder of trunk smooth except for feeble transverse rugae above neck on pronotum and very strongly developed transverse rugae 0.02 to 0.05 mm apart on dorsum of propodeum and extending obliquely across sides; declivitous face of propodeum smooth. Head orange red; clypeus, occipital lobe, legs and trunk reddish orange; petiole yellowish orange; antennae and mandibles orange yellow.

Paratype. One dealate queen, same date and collection number as holotype (BMNH).

Additional Records. BORNEO: Sarawak: Several series from 4th Division, Gunung Mulu National Park: 500 m+, pitfall trap, iv-v-1978, one worker, one dealate queen (I. Hanski, BMNH and MCZ); mixed dipterocarp forest, 2.iii.1978, leaf litter, one worker (H. Vallack, BMNH); v-viii.1978, B.M. 1978-49, camp 5, one dealate queen (P. M. Hammond and J. E. Marshall, BMNH). H. Vallack's specimen larger than holotype (HW 1.10 mm) with node of petiole somewhat taller and more massive, and with a broad shallow concavity between the propodeum and the metathoracic tubercles (but metanotal groove not visible in profile as a distinct notch).

Myrmoteras indicum new species

Figures 4, 7-10, 27, 30; Map 2

Holotype. Worker deposited in MHN from India: Tamil Nadu: Anaimalai Hills, 18 km au nord de Valparai, 1,250 m, 18.XI.1972, #35 [tamisages en forêt] (C. Besuchet and I. Löbl). Name in reference to the country of origin.

Diagnosis. The only species in the *bakeri* group from India. Workers can be distinguished from those of *M. bakeri* by having a single apical denticle and relatively slender tibiae (TWI < 21); and from *M. diastematum* by the lack of a wide sulcus between the clypeus and head capsule; and from both species by the reduced palpal segmentation (3,3 or 4,3).

Worker. Holotype (HW 1.03 mm) and four paratypes from the same locality: TL 5.3 to 5.9, HW 0.94 to 1.05, HL 1.00 to 1.12 (CI 92 to 95), ML 1.53 to 1.70 (MI 100 to 108), SL 1.18 to 1.31 (SI 124 to 127), EL 0.63 to 0.68, HFL 1.22 to 1.26 (TWI 16 to 17), WL 1.53 to 1.60 mm. Frontal sulcus conspicuous but narrow; orbital grooves moderately developed. Frontal area clearly defined. Palpal segmentation 3,3 (10 workers inspected). Mandibles with 11 to 13 teeth (usually 12) and without preapical denticles. Only one apical denticle, although this one is relatively large.

Pronotum low and evenly convex; propodeum evenly rounded, summit higher than mesothorax; metanotal groove not visible as a notch in profile. In several specimens the propodeum balloons out below the level of the spiracle (as occurs in males), but otherwise such individuals appear little different. The propodeum is more conventionally shaped in most paratypes and in all other material associated with this species. Node of petiole moderately thick; anterior face straight and vertical, posterior face less steep and curving gently into summit; summit rounded and moderately wide.

Head smooth, but some workers with traces of longitudinal rugae immediately above clypeus; pronotum smooth; mesonotum with feeble longitudinal rugae present laterally below a conspicuous ruga which extends forward from each metathoracic tubercle; mesonotum dorsally with finely transverse rugae showing traces of granulate sculpture; propodeum virtually smooth but with traces of transverse

rugae dorsally in some; remainder smooth. Pilosity sparse, with less than 10 hairs breaking dorsal margin of trunk when viewed in profile. Hairs rising 0.08 to 0.10 mm on head, trunk and gaster; zero to one hair on or near each metathoracic tubercle and two to five on node of petiole. Reddish orange head, trunk, and gaster (the latter with a touch of brown); petiole and antennae orange yellow; legs and mandibles same but lighter.

Queen. Paratypes from the type series (two measured): TL 6.2, HW 1.11, HL 1.12 to 1.15 (CI 96 to 99), ML 1.66 to 1.68 (MI 144 to 150), SL 1.31 to 1.33 (SI 118 to 120), EL 0.69 to 0.70, HFL 1.40 to 1.41 (TWI 19), WL 1.62 to 1.64 mm. Trunk smooth except for usual transverse rugae on cervix and a row of very short, feeble transverse rugae along median line dorsad on propodeum, not extending onto sides laterally (although surface sometimes indistinctly rugose below level of spiracle on sides).

Male. Paratypes from the same locality as holotype (two measured): HW 0.75, HL 0.85 to 0.86 (CI 87), SL 1.20 to 1.21 (SI 160), EL 0.43, WL 1.40 to 1.44 mm. Frontal sulcus well defined, wide near median ocellus. Scapes long, more than $1.5 \times$ HW. Palpal segmentation same as females. Head and trunk smooth outside of conspicuous irregular rugae on cervix and on propodeum (but smooth beneath propodeal spiracle on sternites, which bulge somewhat).

Paratypes. Twenty-two workers, three alate queens, three dealate queens, and seven males, same locality and collection number as holotype (MHN, MCZ, BMNH, MCSN).

Additional Records. Unless otherwise stated, collected by C. Besuchet and I. Löbl from berlesate samples in forest habitats. INDIA: *Kerala:* Cardamom Hills, entre Pambanar et Peermade, 950 m, 9.XI.1972, #18 [près d'une rivière], seven workers, one alate queen, five dealate queens, one male (MHN, MCZ); Cardamom Hills, Valara Falls, à 46 km au sud-

ouest de Munnar, 450 to 500 m, 25.XI.1972, #49 [près de la rivière], one worker, one dealate queen (MHN, MCZ); Nelliampathi Hills (nord-ouest des Anaimalai Hills), Kaikatty, 900 m, 30.XI.1972, #58 [près d'un ruisseau], thirteen workers, three alate queens, one dealate queen, six males (MHN, MCZ, MCSN). *Tamil Nadu:* Nilgiri Hills, 4,000 ft, 1907-329, one worker (H. L. Andrews, BMNH); Palni Hills, 7 km à l'est de Kodaikanal, 1,750 m, 12.XI.1972, #24, one worker (MHN); Palni Hills, 10 km au nord-ouest de Kodaikanal, 2,150 m, 15.XI.1972, #27 [lisière de forêt, avec rhododendrons et fougères, près d'une rivière], one queen (MHN); Anaimalai Hills, au-dessus d'Aliyar Dam, 1,150 m, 18.XI.1972, #34 [au pied d'un groupe d'arbres envahis par les lianes], eight workers, one alate queen, four dealate queens (MHN, MCZ, MCSN); Anaimalai Hills, Valparai, 1,100 m, 20.XI.1972, #39 [forêt avec cafés], 17 workers (MHN, MCZ); Nilgiri Hills, 6 km à l'est de Coonoor, 1,400 m, 22.XI.1972, #42 [dans un ravin], five workers, one dealate queen, five males (MHN, MCZ); Nilgiri Hills, Coonoor, 1,600 m, 22.XI.1972, #43, five workers, three males (MHN, MCZ); Nilgiri, Hulical près de Coonoor, sur la rive droite de Coonoor River, 1,600 m, 22.XI.1972, #44 [dans un ravin], two workers, two dealate queens (MHN, MCZ).

All the material here ascribed to *M. indicum* is very similar to the type series in most respects. However, the series can be divided into two groups: all females in series 18, 39, and the queen in series 42 have a palpal segmentation of 3,3 and lack preapical denticles, as in the type series. Females in all remaining series (including workers from series 42) consistently have 4,3 palpal segmentation, and at least one (sometimes two) preapical denticles. In addition, in several series in the latter group (specifically 24, 27, 34, 49, and 58) the propodeum of the females is more or less conspicuously transversely rugose (with rugae extending obliquely over sides

and posterior declivity smooth; Figs. 7, 8); in all other series the propodeum is smooth (with traces of rugae in some queens) (Fig. 30).

Further variation between series occurs across both groups: pilosity varying from sparse to dense (with more than 20 hairs breaking dorsal margin of trunk viewed in profile in series, 18, 24, 34, and 58); zero to one hair on or near each metathoracic tubercle, or more than that number (series 18, 34, 49); frontal area not demarcated to well developed (the latter in series 34, 35, 49, and 58); variation in width of the frontal furrow; presence or absence of feeble longitudinal rugae between antennal fossae (best developed in series 58); orbital grooves moderately developed to conspicuous. Randomly selected individuals measured from all series ranged in size from 0.88 to 1.09 mm ($n = 24$), and CI ranged from 92 to 103 in 14 selected individuals.

Natural History and Biogeography. All collections of this species were made at altitudes between 450 and 2,150 m, suggesting *M. indicum* is restricted to higher elevations. This choice of habitat and the consequent fragmentation of the species into numbers of relatively isolated populations could account for the minor character differences between localities. That the series consistently fall out into two groups on the basis of palpal segmentation and preapical denticle number is more difficult to explain and could be evidence for the existence of two sibling species. All the series are from a relatively small area of the Western Ghats and Nilgiris, and the two groups do not separate geographically in any obvious way. The only series with representatives of both groups is #42 (from the Nilgiri Hills).

THE DONISTHORPEI GROUP

Size small to medium. Palpal segmentation 5.4 or 5.3. Head and trunk sculptured as in *williamsi* group, but sculpture relatively delicate. A well-marked narrow ruga which clearly originates at the base

of each metathoracic tubercle extends forward across mesothorax, effectively dividing mesothorax into dorsal and lateral areas. Metanotal groove not visible as a conspicuously impressed notch in profile. Petiole distinctive: sternum highly convex beneath node (Fig. 34).

The group includes two species from Borneo, and apparently also *M. karnyi* from the Mentawai Archipelago.

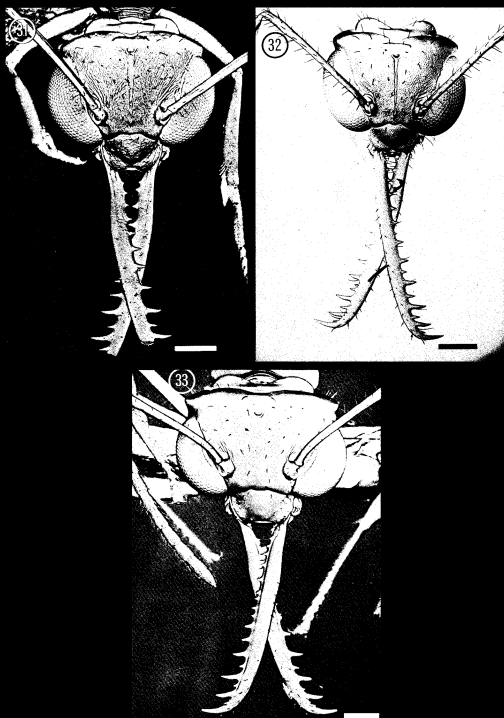
Myrmoter as chondrogastrum new species Figures 31, 34; Map 2

Holotype. Worker deposited in BMNH from Borneo: Sarawak: 4th Division, Gunung Mulu National Park, v-viii.1978, no. 49 (P. M. Hammond and J. E. Marshall B. M. 1978). The specific name derived from *Gr. chondros* + *gaster*, referring to the granulate sculpture on the gaster.

Diagnosis. Similar to *M. donisthorpei*, but the granulate sculpture on the gaster is unique to this species.

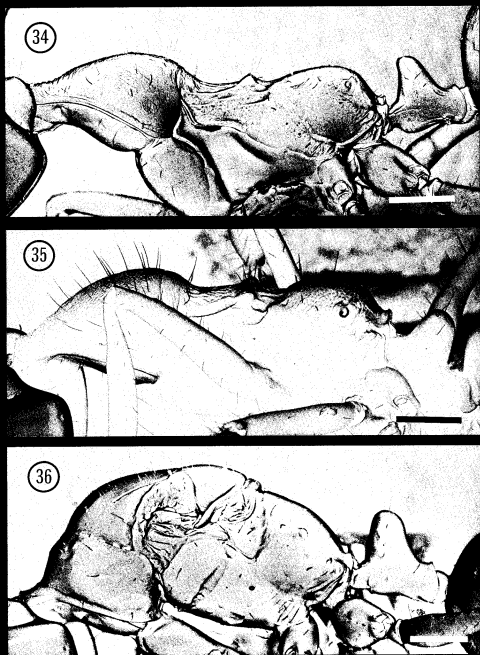
Worker. Holotype: TL 5.3 (est.), HW 0.94, HL 1.00 (CI 94), ML unknown (tips broken), SL 1.12 (SI 119), EL 0.66, HFL 1.20 (TWI 19), WL 1.45 mm. Frontal sulcus a wide trench, somewhat wider than in *M. donisthorpei* (wider midway between epistomal suture and ocelli than diameter of median ocellus); orbital furrows conspicuous. Frontal area clearly defined. Palpal segmentation 5.4. Mandibles with tips broken, probably originally with 12 teeth and 2 preapical denticles, as in queen; condition of apical denticles unknown (in the queen each mandible has a single stout apical denticle). Dorsum of mandibles with a medial groove as in *M. morowali*, but groove more feeble and extending only as far as fourth or fifth tooth from base.

Pronotum low and evenly convex; propodeum somewhat flattened dorsad, although feebly evenly convex, and with summit virtually level with mesonotum. In profile node of petiole with anterior and posterior faces straight, anterior face steep but not vertical, posterior face not as steep, curving more gently into sum-



Figures 31–33. The *donisthorpei* and *insulcatum* groups. Frontal views of the worker head, 31. *M. chondrogastrum* holotype (uncoated). 32. *M. donisthorpei* from Sarawak. 33. *M. insulcatum* (holotype queen, uncoated).

Scale lines, 0.25 mm.



Figures 34–36. The *donisthorpei* and *insulcatum* groups. Lateral views of the worker trunk and gaster. 34, *M. chondrogastrum* holotype (uncoated). 35, *M. donisthorpei* from Sarawak. 36, *M. insulcatum* (holotype queen, uncoated).

Scale lines: 0.25 mm.

mit; summit narrow. Middle and hind tibiae less dilated than in *M. donisthorpei*.

Head finely granulo-rugose, rugae between 0.01 to 0.02 mm across; posterior to median ocellus and beneath head smooth; smooth laterally except for fine vertical rugae near eyes. Frontal area and clypeus feebly granulate. Pronotum granulate, smoother laterally and with transverse rugae near neck; mesonotum with a ruga extending forward from each tubercle, very feebly granulo-rugose dorsally and longitudinally rugose laterally; dorsally propodeum with fine and very feeble transverse rugae, declivity and sides virtually smooth. Gaster very finely and irregularly granulate dorsally; laterally more feebly sculptured and smooth ventrad. Hair density moderate, with 25 hairs breaking dorsal margin of trunk when viewed in profile. Hairs short, rising 0.08 mm on head and 0.10 mm on trunk and gaster; two to five hairs on or near each metathoracic tubercle and six on node of petiole. Head orange; trunk, petiole, and mandibles orange yellow; gaster brownish orange; antennae yellowish orange; legs very light yellow.

Queen. Paratype: TL 5.6, HW 1.00, HL 1.03 (CI 97), ML 1.45 (MI 141), SL 1.15 (SI 116), EL 0.66, HFL 1.23 (TWI 18), WL 1.48 mm. Trunk dorsally with feeble granulate sculpture, tending towards longitudinally granulo-rugose medially on mesonotum; smooth laterally. Propodeum transversely rugose dorsally and obliquely rugose on sides, rugae ca. 0.15 mm apart; declivity smooth.

Paratype. Single dealate queen, same date and collection number as holotype (MCZ).

Additional Records. Known only from type series.

Myrmoteras donisthorpei

Figures 32, 35; Map 2

Myrmoteras donisthorpei Wheeler, 1916: 14, fig. 3. Borneo: West Sarawak: Mt. Matang, 16.1.1914, 1 alate queen (G. E. Bryant, MCZ [examined]).

Emery, 1925: pl. 1, fig. 16. Creighton, 1930: 187, pl. 11, fig. 3.

Diagnosis. With the distinguishing characteristics of the *donisthorpei* group and a smooth and shining gaster, and with summit of propodeum not higher than the mesonotum.

Worker. Described for the first time from several series from Borneo. TL 4.5 to 4.8, HW 0.83 to 0.90, HL 0.82 to 0.91 (CI 97 to 101), ML 1.20 to 1.38 (MI 146 to 154), SL 0.84 to 0.98 (SI 102 to 109), EL 0.56 to 0.61, HFL 0.83 to 0.95 (TWI 24 to 27), WL 1.19 to 1.28 mm. Frontal sulcus a narrow groove; orbital furrow moderately conspicuous. Frontal area present but poorly demarcated. Palpal segmentation 5.4 in two workers from Sarawak and 5.3 in the worker from Sabah. Workers from Sarawak and Sabah with 12 to 13 teeth and 2 to 4 preapical denticles (usually 2 to 3); single worker from Kalimantan with 10 teeth and 3 preapical denticles on both mandibles. Apical denticle pair small in size, the smallest very tiny and closely applied to the slender, more apical denticle.

Trunk as described for *M. chondrogastrum* except in side view with a wide, shallow concavity between metathoracic tubercles and propodeum (but metanotal groove not visible as a conspicuously impressed notch in profile). Petiole also very similar, but with anterior face of node closer to vertical; summit broader. Tibiae strongly dilated.

Head (including frontal area and clypeus) longitudinally granulo-rugose, with sculpture extending back to about as far as median ocellus, rugae ca. 0.01 mm across; smooth on occiput, laterally beneath eyes (except for feeble vertical rugae near eyes) and under head. Pronotum transversely granulo-rugose, sculptured more feebly on sides; mesothorax longitudinally granulo-rugose dorsad, laterally with three to five narrow longitudinal rugae on smooth surface; propodeum feebly granulate, declivity very feebly trans-

versely granulo-rugose to smooth. Hair density moderate, with 17 to 26 hairs breaking dorsal margin of trunk when viewed in profile. Hairs short, rising 0.06 to 0.08 mm on head and 0.10 mm on trunk and gaster; two to three hairs on or near each metathoracic tubercle and five to seven on node of petiole. Mostly orange red to reddish orange, with head slightly lighter colored and legs reddish orange with femora, trochanters, and sometimes the coxae virtually white; antennae and mandibles orange yellow. Sabah specimen very dark orange red, including legs.

Queen. Holotype: TL 4.5, HW 0.85, HL 0.88 (CI 97), ML 1.26 (MI 144), SL 0.91 (SI 107), EL 0.58, HFL 0.88 (TWI 24), WL 1.20 mm. Both mandibles with 12 teeth and two preapical denticles (Sarawak queen with 11 to 12 teeth). Less strongly sculptured than described for Sarawak workers, with sculpture on head rugulose, rugae ca. 0.01 mm in width; clypeus more feebly and irregularly rugulose; trunk virtually smooth, very feebly granulate on mesonotum; propodeum transversely rugose dorsally (rugae 0.02 to 0.03 mm apart), obliquely rugose on sides, and with declivity virtually smooth. Coloration similar to workers but femora not as pale.

Male. Described for the first time from a Sarawak specimen: HW 0.59, HL 0.65 (CI 91), SL 0.78 (SI 132), EL 0.34, WL 0.98 mm. Frontal sulcus a feebly impressed medial line. Papal segmentation 6.4. Head smooth except for a trace of granulate sculpture low on face; clypeus feebly granulate. Trunk granulate; propodeum with a denser network of rugae than in *M. williamsi*; these continue onto declivity. Traces of granulate sculpture on petiole.

Additional Records. BORNEO: Sarawak: 4th Div., Gunung Mulu National Park, v-viii 1978, B. M. 1978-49, camp 1 [three workers, one dealate queen, one male]; camp 5 [one worker] (P. M. Hammond and J. E. Marshall, BMNH and

MCZ); *ibid.*, limestone forest, 27.v.78 pitfall trap, one worker (H. Vallack, BMNH). Sabah: Gunung Silam 880 m, 1983, A19 9.2, one worker (R. Leakey, BMNH). S. E. Kalimantan: 17-46 km W Batulitjin, 28 June-2 July 1972, lowland rainforest, soil under litter, one worker (W. L. Brown, MCZ). Queen from Batulitjin (HW 0.92) larger than holotype but likewise with measurements and indices within range shown by the workers; sculpturing stronger than holotype: head granulo-rugose, pronotum, mesonotum, and scutellum granulate.

Myrmoteras karnyi

Map 2

Myrmoteras karnyi Gregg, 1954: 23, fig. 1. Indonesia: Mentawai Archipelago: Sipora Island, 22C, 31 October 1924 (H. H. Karny. Deposited in Zoologisch Museum en Laboratorium, Bogor; holotype not found).

Diagnosis. Apparently similar to *donisthorpei*, but with pronotum and propodeum relatively very high and convex: summit of propodeum higher than mesonotum, and as high as summit of pronotum.

Worker. No specimens seen. Can be assigned to *Myagroteras* from examination of figure in Gregg (1954), which is relatively detailed and is assumed to be accurate. The figure shows a conspicuous frontal sulcus, mandibles only very feebly curving ventrad near tips, and the lack of trigger hairs and projecting triangular labrum. I tentatively place *M. karnyi* in the *donisthorpei* group because of the strong convex curvature of the sternum of the petiole, as judged by the illustration of Gregg (1954). Also the sculpture, although apparently not granulate as in the other species in this group, is much better developed than in species of the *bakeri* group. However, the conformation of the trunk apparently bears a resemblance to *M. williamsi*, and it is possible that *karnyi* belongs in the *williamsi* group.



Figure 37. Labral structure, *M. insulicatum* (uncoated holotype). Arrow indicates one of the long labral hairs.

Scale line, 0.05 mm.

The following is based on the description of Gregg and the figure which accompanies it: frontal furrow a narrow, conspicuous groove; orbital furrows narrow, moderately conspicuous (in drawing

appearing much as in *donisthorpei*). Mandibles with 10 teeth and two apical denticles, but apparently lacking preapical denticles. Head dorsally with narrow longitudinal "striations or rugulae" from

margin of clypeus to well above antennal bases, behind this apparently smooth; rugae straight except where they curve around the antennal insertions. Pronotum higher and more strongly convex than in *M. donisthorpei* and *chondrogastrum*; mesothorax with "strong longitudinal rugae," and strongly depressed relative to pronotum and propodeum, "recalling the condition in *williamsi*"; propodeum as high as the pronotum and strongly convex, and from drawing apparently longitudinally rugose. Pilosity on trunk apparently at least moderately dense. Petiole strongly convex beneath node; node apparently narrower than in *donisthorpei* or *chondrogastrum*. Middle and hind tibiae relatively slender, with the drawing comparing favorably with *chondrogastrum*, and unlike the strongly dilated condition in *donisthorpei*. Color unknown.

Length in original description given as 3.6 mm. However, judging from the value Gregg gives for the length of the *M. ceylonicum* holotype (Gregg, 1956), his measure of total length does not include ML; TL therefore estimated as 4.5 to 4.6 mm. "Head index" given as 0.92, but the value of this index given by Gregg (1956) for *ceylonicum* holotype is much lower than that calculated given the definition of cephalic index used here; calculation based on Gregg's illustration of *karnyi* yields a CI of 97. These estimates of the TL and CI values compare very favorably to the values for *M. donisthorpei*.

THE INSULCATUM GROUP

Head and trunk highly polished, lacking sculpture. No trace of frontal sulcus on head (sulcus conspicuous in all other species in the subgenus). Clypeus only

feebly convex medially, as in most species in the subgenus *Myrmoteras*. The two labral hairs presumed homologous with the trigger hairs of the subgenus *Myrmoteras* are more widely separated than in any other species of *Myagrotas* (Fig. 37). Palpal segmentation 3.3. Mandibles with 14 to 15 teeth, the highest number recorded.

Known only from a single dealate queen from the Philippines.

Myrmoteras insulcatum new species

Figures 33, 36, 37; Map 2

Holotype. Dealate queen deposited in MCZ from Philippines: Luzon: Lagunas: Mt. Makiling, ca. 150 m below summit, litter, Feb. 1968 (R. A. Morse). Name from Latin *in + sulcus*, referring to the lack of a frontal sulcus.

Diagnosis. The only species of *Myagrotas* completely lacking a frontal sulcus.

Queen. Holotype: TL 5.6, HW 1.07, HL 1.01 (CI 106), ML 1.53 (MI 152), SL 1.08 (SI 100), EL 0.61, HFL 1.16 (TWI 22), WL 1.54 mm. Orbital grooves moderately developed. Frontal area present but somewhat poorly demarcated. Palpal formula 3.3. Mandibles with 14 to 15 teeth and two preapical denticles. Apical denticles both tiny, the smallest very tiny and closely applied to the larger, which is closely applied in turn to the apical tooth. A feeble groove extends longitudinally down the dorsal surface of mandible to at least penultimate tooth, but unlike other ants with such a groove (*M. morowali*, *diastematum*, and some *bakeri*), the groove extends very close to inner, toothed margin (Fig. 37).

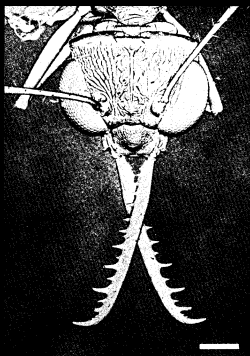
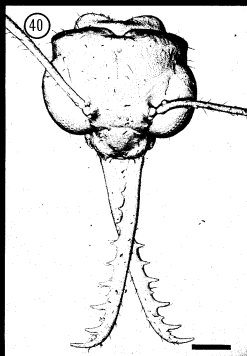
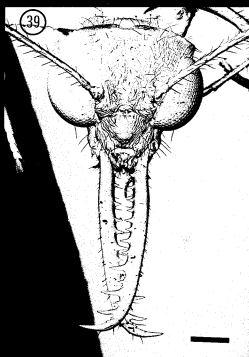
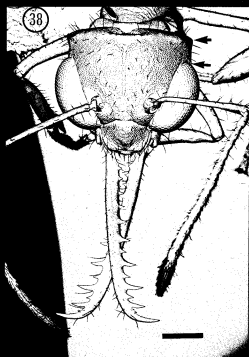
Node of petiole with straight, nearly vertical anterior face, posterior face steep

Figures 38–41. The *williamsi* group. Frontal views of the worker head. 38. *M. morowali* paratype (arrows indicate postocular distance). 39. *M. toro* paratype. 40. *M. williamsi* (from Negros; specimen oily). 41. *M. wolasi* holotype (uncoated).

Scale lines: 0.25 mm.

Figures 42–45. The *williamsi* group. Lateral views of the worker trunk and gaster. 42. *M. morowali* paratype (arrow indicates location of metanotal groove). 43. *M. toro* paratype. 44. *M. williamsi* (from Negros; specimen oily). 45. *M. wolasi* holotype (uncoated).

Scale lines: 0.25 mm.





and curving; summit wide and rounded. Ventral margin of petiole feebly convex beneath node.

Head, trunk and gaster entirely smooth and very highly polished. Hair density moderate; hairs short and moderately abundant, rising 0.08 mm on head, 0.14 mm on trunk and gaster; eight hairs on node of petiole. Dark orange red, with clypeus and occipital lobe somewhat lighter, mandibles orange yellow, legs and antennae reddish orange.

Additional Records. Known only from holotype.

THE WILLIAMS GROUP

Size small to medium (known range of females: TL 4.2 to 5.0 mm, except *M. toro* 5.2 to 5.6 mm). Head and pronotum strongly granulate or granulo-rugose. Orbital grooves moderately developed, less conspicuous than in other *Myagrotas* species. Postocular distance at least 20% of eye length (narrower in all other species in the genus). Palpal segmentation 6.4 (at least two workers in each species inspected where available). Lacking a conspicuous narrow ruga extending forward along sides of mesonotum from base of each metathoracic tubercle. Metanotal groove usually conspicuously impressed. Sternum of petiole feebly convex beneath node.

This group includes three closely related species from Sulawesi, all of which are new. These represent the first records of the genus *Myrmoteras* for Sulawesi, which now is the farthest the genus is known to extend to the southeast. In addition, I include here the distinctive Philippine species *M. williamsi*.

Myrmoteras morowali new species

Figures 38, 42; Map 2

Holotype. Worker deposited in BMNH from Indonesia: Central Sulawesi: near Morowali, Ranu river area, 27.i.-20.iv.1980, B.M. 1980-280 (M. J. D. Brendell). Name is a noun in apposition after the type locality.

Diagnosis. Distinguished from closely related *M. wolasi* and *M. toro* by the fine-

ly granulate sculpture dorsally on head and pronotum; very smooth and shining frontal area; granulate clypeus; presence of transverse rugae across declivity of propodeum, which is smooth only near base; and light yellow color, with the petiole concolorous with trunk and gaster.

Worker. Holotype (HW 0.80) and four paratypes: TL 4.2 to 4.5, HW 0.80 to 0.82, HL 0.83 to 0.85 (CI 96 to 97), ML 1.13 to 1.19 (MI 140 to 144), SL 0.87 to 0.90 (SI 108 to 112), EL 0.49 to 0.50, HFL 0.87 to 0.93 (TWI 22 to 23), WL 1.15 to 1.20 mm. Frontal sulcus a very narrow, well-defined groove. Frontal area very clearly defined. Mandibles with 11 to 12 teeth (usually 11) and two to four preapical denticles (usually three). Smallest apical denticle tiny, closely applied to the larger denticle, which is small and sharp. Mandibles with feeble but conspicuous medial grooves extending longitudinally for most of the length of the shafts (absent in *M. wolasi*).

Trunk very similar to *M. toro*, except propodeum dorsally flattened and with posterior slope of petiole relatively straight, curving only at base and summit. Metanotal groove conspicuously impressed but narrower than in *M. toro*.

Finely and regularly granulate dorsally on head and clypeus, also granulate (but more feebly) on back of head, including occipital lobe; granules ca. 0.01 mm across. Frontal area smooth and translucent, and thus standing out prominently. Sides of head below eyes longitudinally granulo-rugose; ventral surface of head smooth. Pronotum granulate, granules formed into broad longitudinal rugae, particularly dorsad; mesonotum densely longitudinally rugose, with traces of granulate sculpture, pleura of mesothorax with similar, but less dense rugae, granulate sculpture absent; propodeum with longitudinal granulate rugae, declivity transversely rugose except near base. Pilosity dense, with 30 to 36 hairs breaking dorsal margin of trunk in profile. Hairs short, rising to 0.06 to 0.08 mm on head and 0.10 mm on trunk and gaster. Two or three hairs at or near each metathoracic tubercle; node of peti-

ole with four to eight hairs. Color exceptionally light, uniform yellow or orange yellow, mandibles somewhat lighter.

Queen. TL 4.5, HW 0.80, HL 0.83 (CI 97), ML 1.13 (MI 137), SL 0.86 (SI 107), EL 0.48, HFL 0.90 (TWI 22), WL 1.21 mm. Dorsum of trunk granulate, with the mesonotum and scutellum longitudinally granulo-rugose; mesepisternum much smoother; propodeum with strong narrow transverse rugae 0.02 to 0.03 mm apart, smooth low on declivity. Uniform yellowish orange.

Paratypes. One dealate queen and four worker paratypes with same locality data and collection number (BMNH and MCZ).

Additional Records. Known only from type series.

Myrmoteras toro new species

Figures 1, 39, 43, 46, 47; Map 2

Holotype. Worker deposited in MCZ from Indonesia: Central Sulawesi: Lore Lindu National Park at Toro, 82 km south of Palu, disturbed rainforest, single cluster of ants in loose leaf litter, 15.VII.1983 (M. W. Moffett). The specific name is a noun in apposition after the type locality.

Diagnosis. Can be distinguished from *M. wolasi* and *morowali* by its larger size, the lack of granulate sculpture on the clypeus, and the relatively more rounded propodeum.

Worker. Holotype (HW 1.01 mm) and paratypes: TL 5.2 to 5.6, HW 0.97 to 1.05, HL 0.97 to 1.03 (CI 100 to 102), ML 1.48 to 1.58 (MI 153 to 154), SL 1.07 to 1.15 (SI 109 to 110), EL 0.58 to 0.62, HFL 1.13 to 1.18 (TWI 19 to 22), WL 1.35 to 1.56 mm (eight measured). A medium-sized species. Frontal sulcus narrow (0.01 to 0.02 mm wide), anterior to antennal bases weak and difficult to distinguish from the heavy sculpturing. Frontal area poorly demarcated, unlike *M. morowali*. Mandibles with 11 to 13 teeth (usually 12) and two to three preapical denticles. Apical denticles tiny and not greatly different in size; the most apical is closely applied to the apical tooth. Mandibles dorsally without any trace of feeble grooves found in *M. wolasi*.

Pronotum low and convex; propodeum evenly convex (except for somewhat abrupt declivity), summit virtually level with mesonotum. Metanotal groove conspicuously impressed. Node of petiole with vertical anterior slope and steep but more curving posterior slope; node narrow. Petiole feebly convex beneath node.

Dorsum of head densely packed with very wavy, ca. 0.02 mm wide rugae, which encircle antennal bases and proceed otherwise more or less longitudinally; back of head (behind ocelli) feebly rugulose, with rugae radiating out from along dorsal and lateral margins of occipital lobe, and with similar rugae on the lobe itself, particularly mesad; clypeus with feeble longitudinal rugae laterally, smoother medially, without granulate sculpture; frontal area feebly irregular. Finely longitudinally rugose on sides below eyes; smooth beneath head. Pronotum with very irregular, sinuous rugae, thicker and more widely separated than those on head. Mesothorax and propodeum with rugae ca. 0.03 to 0.04 mm apart, these mostly more or less longitudinal (oblique laterally on mesothorax), katapisternum, mesonotum, and dorsum of propodeum with rugae less distinct; declivity of propodeum with irregular transverse rugae near summit, below that virtually smooth. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk when viewed in profile. Hairs rising 0.10 to 0.12 mm on head, trunk and gaster; two to three hairs on or near each metathoracic tubercle and five to nine on node of petiole. Most workers uniformly very dark orange red; mandibles, tarsi, and trochanters yellowish orange. Two teneral individuals have orange yellow to reddish yellow heads, trunks and legs, gasters brownish orange, and antennae, mandibles, trochanters and tarsi orange yellow.

Queen. See Figure 46. TL 5.5, HW 1.03, and other measurements within the range shown by workers. Dorsum of trunk granulate, with the mesonotum and scutellum longitudinally granulo-rugose; pleura relatively smooth; propodeum transversely rugose.

Paratypes. Workers and dealate queen from same colony (MCZ, BMNH, MHN, MCSN).

Additional Records. Known only from type series.

Natural History. The type series apparently represents a complete colony consisting of 22 workers and one queen, which was collected between loose leaves in the leaf litter on the forest floor. In captivity the ants foraged solitarily for various soft bodied invertebrate prey, which they captured with their trap-like jaws (Fig. 47).

Myrmoteras williamsi

Figures 40, 44; Map 2

Myrmoteras williamsi Wheeler, 1919: 146. Philippine Islands: Luzon: Los Baños, 2 alate queens, 1 male (F. X. Williams, MCZ, queens examined, male missing). Creighton, 1930: 189, fig. 2, pl. 11, fig. 4, worker described.

Diagnosis. Shape of the trunk in workers distinctive: pronotum and propodeum high and strongly convex; mesothorax relatively depressed. *M. williamsi* has only been collected in the Philippines. *M. karnyi* (tentatively placed in the *donisthorpei* group) has a somewhat similarly shaped trunk, but the head and trunk of this species are apparently not strongly granulate (Gregg, 1954).

Workers. Known only from Negros. Two measured (numbers in brackets indicate measurements that could only be taken on the smaller specimen): TL [5.0], HW 0.95 to 1.00, HL 0.95 to 1.00 (CI 100), ML 1.38 to 1.50 (MI 145 to 151), SL [1.10] (SI [113]), EL 0.55 to 0.58, HFL 1.05 to 1.18 (TWI [21]), WL 1.30 to 1.40 mm. Frontal sulcus very narrow but well defined. Frontal area present but poorly demarcated. Clypeus less strongly convex medially than in most other *Myagrotas* species, although not as flattened as in most *Myrmoteras*. Palpal segmentation 6.4 (two workers inspected). Mandibles with 11 to 13 teeth and two preapical denticles. Apical denticles small, the smallest tiny, but conspicuous, the largest closely applied to

apical tooth for much of its length. Mandibles bent more strongly ventrad at penultimate tooth than in other *Myagrotas*, but not as strongly as in subgenus *Myrmoteras*.

Both pronotum and propodeum very high and rounded (except declivity of propodeum virtually straight), so that mesonotum appears relatively very depressed. In profile with a wide concavity between metathoracic tubercles and propodeum, but metanotal groove not visible as a conspicuously impressed notch in profile. Petiole with steep to nearly vertical anterior slope; posterior slope less steep, straight but curving gently up to summit.

Head (including frontal area and clypeus), pronotum and propodeum finely and evenly granulate, granules 0.01 to 0.02 mm across, present as well on back of head and laterally beneath eyes, and with traces of granular sculpture beneath head; declivity of propodeum smooth; mesothorax with feeble granulate sculpture, widely separated narrow longitudinal rugae on sides and virtually smooth above; funiculi, mandibles and legs feebly granulate, with the sculpture strongest on the tibiae; petiole and gaster smooth. Pilosity sparse to moderate, with 6 to 18 hairs breaking dorsal margin of trunk when viewed in profile (but specimens in very poor condition and conceivably have lost hairs). Hairs short, rising 0.06 mm on head, trunk and gaster; one to two hairs on or near each metathoracic tubercle and two to three on node of petiole. Head and trunk reddish orange (except clypeus and occiput orange red); petiole same but slightly lighter; gaster brownish or yellowish orange; legs yellowish orange; mandibles and antennae orange yellow.

Queen. Syntypes (two measured): TL 4.4 to 5.0, HW 0.91 to 0.96, HL 0.88 to 0.93 (CI 103), ML 1.15 to 1.18 (MI 127 to 130), SL 0.91 to 0.94 (SI 99 to 100), EL 0.53 to 0.56, HFL 0.89 to 1.00 (TWI 19 to 22), WL 1.18 to 1.28 mm. Hairs moderately dense and longer than in Dumaquete worker specimens (0.08 to 0.10 mm). Trunk finely and evenly granulate, pro-



Figures 46–47. *Myrmoteras toro* paratypes. 46. Queen. 47. Forager carrying a mosquito, which it had captured after the author dropped the prey, wounded, in front of it.

podeum transversely granulo-rugose, including on declivity. Funiculi, mandibles and legs smooth.

Male. Single male from Mt. Makiling: HW 0.68, HL 0.75 (CI 91), SL 0.84 (SI 124), EL 0.38, WL 1.2 mm. Frontal sulcus a shallow groove beginning well above clypeus and ending before reaching median ocellus. Maxillary palpi with six segments. Head and trunk granulate; longitudinally granulo-rugose dorsad on mesonotum, more feebly granulate laterally; propodeum feebly granulate with a conspicuous network of raised ridges, except declivity virtually bare outside of medial ruga.

Additional Records. PHILIPPINES: *Luzon:* Benguet, Baguio, one alate queen (C. F. Baker, BMNH); Mt. Makiling, one alate queen, one male (C. F. Baker, BMNH and MCZ). *Negros Oriental:* Dumaguete: Camp 4.6.1927; Camp 4.2.1931; Lake 4.30.1931 [each with one worker] and 5.18.1927 [one dealate queen] (J. W. Chapman, MCZ). Specimens from Negros have relatively longer mandibles (MI 139 to 151, compared with 124 to 130 for Luzon specimens) and scapes (SI 110 to 111 compared with 99 to 100). Also, the Negros specimens have a feeble granulate sculpture on the legs, scapes, and mandibles lacking in Luzon material. Negros queen with propodeum more evenly granulate than in types (granules only feebly arranged in transverse rugae); declivity of propodeum smooth near base.

Natural History. Little is known, but J. W. Chapman (in Creighton, 1930) indicated that the ants are "slow and clumsy in movement." F. X. Williams (in Wheeler, 1922) reported that the species nests in the soil.

Myrmoteras wolasi new species

Figures 41, 45; Map 2

Holotype. Worker deposited in MCZ from Indonesia: S.E. Sulawesi: rainforest 1-2 km east of Wolasi, 42 km south of Kendari, ca. 350 m, 13-14 July

1972 (W. L. Brown). The specific name is a noun in apposition after the type locality.

Diagnosis. Distinguished from *M. morowali* and *M. toro* by the presence of distinct granulate sculpture on both the clypeus and frontal area (head and pronotum otherwise conspicuously rugose); declivity of propodeum entirely smooth; and color darker, with petiole strikingly lighter in color than trunk or gaster. Also distinguished from *M. toro* by its smaller size and dorsally flattened propodeum.

Worker. Holotype: TL 4.5, HW 0.88, HL 0.88 (CI 100), ML 1.23 (MI 141), SL 0.96 (SI 109), EL 0.55, HFL 0.98 (TWI 21), WL 1.20. Frontal sulcus a narrow groove, and, like orbital grooves, somewhat wider and more conspicuous than in *M. toro*. Frontal area clearly defined. Both mandibles with 12 teeth and two denticles. Apical denticles both tiny, with little difference in size as in *M. toro*. Mandibles dorsally without any trace of the feeble medial grooves found in *M. morowali*.

Shape and conformation of trunk and petiole exactly as described for *M. morowali*, but with node of petiole narrower.

Sculpture on head similar to *M. toro*, but with rugae wider, 0.03 mm across; rugae longitudinal but diverging somewhat towards occiput. Clypeus and frontal area evenly granulate throughout, not rugose; granules ca. 0.01 mm wide. Back of head smooth except for a few rugae directly behind ocelli; feebly rugulose on occipital lobe as in *M. toro*. Fine longitudinal rugae on sides below eyes; smooth beneath head. Pronotum similar to *M. toro*, with rugae like those on head but more sinuous, mostly transverse caudad and mostly longitudinal farther back and on sides; mesothorax and propodeum rugose as described for *M. toro*, but with declivity entirely smooth. Pilosity very dense, as described for *M. toro*. Head and trunk orange red, petiole (as well as legs and antennae) contrasting yellowish orange, tarsi and mandibles orange yellow.

Additional Records. Known only from holotype.

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LITERATURE CITED

- BINGHAM, C. T. 1903. Hymenoptera. Vol. 2. Ants and cuckoo-wasps. In W. T. Blanford (ed.), Fauna of British India, including Ceylon and India. Taylor and Francis, London, xix + 506 pp., 1 pl.
- BROWN, W. L., JR., AND W. L. NUTTING. 1949. Wing venation and the phylogeny of the Formicidae (Hymenoptera). Trans. Amer. Ent. Soc., 75: 113-131, pl. 8-9.
- CARLIN, N. C. 1983. Polymorphism and division of labor in the dacetina ant *Orectognathus versicolor* (Hymenoptera: Formicidae). Psyche, 88(3-4): 231-244.
- CREIGHTON, W. S. 1930. A review of the genus *Myrmoteras* (Hymenoptera: Formicidae). J. N.Y. Ent. Soc., 38: 177-192, 1 pl.
- EISNER, T. 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). Bull. Mus. Comp. Zool., 116(8): 439-490, pl. 1-25.
- EMERY, C. 1925. Hymenoptera. Family Formicidae, subfamily Formicinae. In P. Wytsman (ed.), Genera Insectorum, fasc. 183. V. Verteneuil and L. Desmet, Brussels, 302 pp., 4 pl.
- FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool., 19: 83-92.
- FELSENSTEIN, J. 1982. Numerical methods for inferring evolutionary trees. Q. Rev. Biol., 57: 379-404.
- FOREL, A. 1893. Note preventive sur un nouveau genre et une nouvelle espèce de Formicide. Ann. Soc. Ent. Belg., 37: 607-608.
- . 1894. Formicides de l'empire des Indes et de Ceylon. J. Bombay Nat. Hist. Soc., 8: 419.
- GOTWALD, W. H., JR. 1969. Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). Cornell Exper. Station Memoir 408, 150 pp.
- . 1973. Mouthpart morphology of the African ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae). J. N.Y. Ent. Soc., 81(2): 72-78.
- GREGG, R. E. 1954. Geographical distribution of the genus *Myrmoteras*, including the description of a new species (Hymenoptera: Formicidae). Psyche, 61(1): 20-30.
- . 1956. A new species of *Myrmoteras* from Ceylon (Hymenoptera: Formicidae). Psyche, 63(2): 41-45.
- HARRIS, R. A. 1979. A glossary of surface sculpturing. Occasional papers in entomology, California Dept. Food and Agriculture, No. 28, 31 pp.
- MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool., 33(1): 83-103.
- WHEELER, W. M. 1916. Four new and interesting ants from Borneo and Luzon. Proc. New England Zool. Club, 6: 9-18.
- . 1919. The ants of Borneo. Bull. Mus. Comp. Zool., 63(3): 43-147.
- . 1922. Observations on *Gigantiops destructor* Fabricius and other leaping ants. Biol. Bull., 42(4): 185-201.
- . 1933. A new *Myrmoteras* from Java. Proc. New England Zool. Club, 13: 73-75.